

Linguistic laws in chimpanzee gestural communication

Heesen, Raphaela^{1,2,*}, Hobaiter, Catherine³, Ferrer-i-Cancho, Ramon⁴, Semple, Stuart¹

¹ Centre for Research in Evolutionary, Social and Interdisciplinary Anthropology, University of Roehampton, London SW15 4JD

² Institut de Psychologie du Travail et des Organisations, Université de Neuchâtel, Rue Emile-Argand 11, CH - 2000 Neuchâtel

³ School of Psychology and Neuroscience, University of St Andrews, St Andrews, Fife KY16 9JP

⁴ Complexity and Quantitative Linguistics Laboratory, Laboratory for Relational Algorithmics, Complexity, and Learning Research Group, Departament de Ciències de la Computació, Universitat Politècnica de Catalunya, 08034 Barcelona, Catalonia, Spain

*Correspondence: raphaela.heesen@unine.ch; +41 32 718 11 90

Abstract

Studies testing linguistic laws outside language have provided important insights into the organisation of biological systems. For example, patterns consistent with Zipf's law of abbreviation (which predicts a negative relationship between word length and frequency of use) have been found in the vocal and non-vocal behavior of a range of animals, and patterns consistent with Menzerath's law (according to which longer sequences are made up of shorter constituents) have been found in primate vocal sequences, and in codons, genes, proteins and genomes. Both laws have been linked to compression – the information theoretic principle of minimising code length. Here, we present the first test of these laws in animal gestural communication. We initially did not find the negative relationship between gesture duration and frequency of use predicted by Zipf's law of abbreviation, but this relationship was seen in specific subsets of the repertoire. Furthermore, a pattern opposite to that predicted was seen in one subset of gestures – whole body signals. We found a negative correlation between number and mean duration of gestures in sequences, in line with Menzerath's law. These results provide the first evidence that compression underpins animal gestural communication, and highlight an important commonality between primate gesturing and language.

Keywords Linguistic laws, compression, information theory, gestures, play.

Introduction

The investigation of linguistic laws – the common statistical patterns of human language – is a cornerstone of quantitative linguistics [1,2]. In recent years, studies have begun to explore the universality of linguistic laws beyond our own species, and this work has provided important insights into the basic rules of organisation underpinning natural information systems. Most notably, exploration of two such laws – Zipf’s law of abbreviation and Menzerath’s Law – has provided evidence that compression, the information theoretic principle of minimising the length of a code, is a universal principle not only of human language, but also of animal behaviour and a range of other biological information systems [3–5].

Zipf’s law of abbreviation predicts a negative relationship between the length of words and how often they are used [6,7]. It is prevalent across a very wide range of human languages [8], being found in written texts (i.e., in character-based [9,10] as well as letter-based writing systems [8]), in speech [11] and in sign language [12]. Patterns consistent with this law – i.e. an inverse relationship between signal magnitude and frequency of use – have also been documented in the behaviour of a number of animal species: the vocal repertoire of Formosan macaques [5], close-range calls of common marmosets [13], social calls of bat species [14], and non-vocal surface behaviour of dolphins [15].

Menzerath’s law predicts that “the greater the whole, the smaller its constituents” and in language holds at different scales of analysis: in words with more syllables, average syllable length is shorter [16], and in sentences with more clauses, average clause length is shorter [12]. A negative relationship between construct and constituent size has been found in the vocal sequences of male geladas [4] and chimpanzees [18], and at the molecular level – between chromosome number and size across species [19], between exon number and size in genes [20], and between domain number and size in proteins [21].

Mathematical explorations indicate that both these linguistic laws reflect compression, and it has been proposed that this is a universal principle driving coding efficiency [3,4,22]. Further corroboration for the effect of compression in the context of Zipf's law of abbreviation can be found by testing whether mean code length is significantly small in signalling systems that follow this law [3]. This has been found to be the case in human language and in animal systems where this law holds [3]. With respect to Menzerath's law, an equivalent corroboration has not yet been conducted (in humans or other species).

Although evidence for compression has been found in a range of natural systems, it is important to expand the range of communicative modes in which this principle is investigated if its true extent is to be assessed. Gestural communication is an important signalling mode in anthropoid primates, including humans [23], and it has been proposed that during human evolution, gestural communication played a key role in facilitating the emergence of spoken language [23]. Gestures are defined as nonverbal communication forms involving visible, manual and bodily actions; they typically occur in short-range communication and are used across a diverse range of social interactions including play, sex, aggression, nursing and grooming [24]. Among the best studied primate gestural systems is that of the chimpanzee, a species known for its extensive gesture repertoire, with gestures given singly or flexibly combined in sequences [25]. Chimpanzees produce 50-70% of the gestures from their repertoire during social play [24,25], and this provides a powerful context to test for compression, at the level of both individual gestures and sequences of these signals.

Here, we analyse a comprehensive dataset on play gestures collected from a wild chimpanzee community, to test Zipf's law of abbreviation in individual gesture types and Menzerath's law in gesture sequences. To complement these two tests for compression, we also test whether mean code length is significantly small in individual gestures and sequences respectively. This study tests these linguistic laws in a mode of animal signalling in which they

have not previously been investigated, and provides the first test of Menzerath's law in the gestural signalling of any species, including humans. Moreover, as these two laws have not been tested simultaneously in the same system outside our own species, our findings provide new insights into the different levels of signal organisation at which compression may be prevalent in systems beyond human language.

Methods

a) Study site and subjects

We conducted observations on the chimpanzees of the Sonso community in Budongo Forest Reserve, Uganda. At the time of study, the community consisted of 81 identifiable members. We defined age classes as: infants (0-4 years), juveniles (5-9 years), sub-adults (female: 10-14 years, male: 10-15 years) and adults (female: ≥ 15 years; male: ≥ 16 years).

b) Data collection

We collected data in four field periods – October 2007–March 2008; June 2008–January 2009; May 2009–August 2009; January 2011–August 2011 – using focal behavioural sampling [26], with observations conducted from 7.30am-4.30pm. We recorded instances of gestural communication during social play using a Sony Handycam (DCR-HC-55). Social play was defined as situations where two or more individuals engaged in play activities indicated by signs of laughter, play-face, and typical body actions such as wrestling, chasing, play-biting or tickling [27].

c) Coding

In total, we analysed 359 video clips for play gestures that met at least one of the key criteria for intentional communication; (i) sensitivity to the receiver's attentional state, (ii) response waiting, or (iii) goal persistence [28]. For each such gesture, we recorded gesture type [58 types were observed in total – ESM, S1], identity of signaller, gesture duration, and time between gestures if gestures were given in sequence.

Measuring gesture duration. We measured gesture duration in frames, with each frame lasting 0.04s, using MPEG Streamclip (v Squared 5, 2012). We determined gesture start as the commencement of movement of body parts participating in the gestural process. We recorded gesture end either as the cessation of the body movements creating the gesture or as the change of body position if the gesture relied on certain body alignments. If the signaller remained in the gesture position while starting to play, we used this as the gesture's end point, as the gesture no longer met criteria for intentional communication [28].

Intra-observer reliability. As all video clips were analysed by one person (RH), to test intra-observer reliability, we randomised the order of clips and remeasured the duration of gestures of every 9th clip ($n=102$ gestures from 37 clips). An intraclass correlation coefficient (ICC) test – Class 3 with $n=1$ rater [29] – revealed very high agreement on measurements of gesture duration ($ICC=0.975$, $p < 0.0001$).

Defining gesture types and tokens. Linguists distinguish between types and tokens [30,31]. To illustrate this, consider the line from Gertrude Stein's poem Sacred Emily [31]: *Rose is a rose is a rose is a rose*. The line includes ten words, and three different types of word. The *types* are the three word types: *rose*, *is*, *a*. The *tokens* represent the overall word count: ten words. In research related to compression, types are used to test Zipf's law of abbreviation and to calculate mean duration, denoted L [3,5,13,15]. Tokens are used to test Menzerath's law and to calculate the total duration of tokens, denoted M [4]. We therefore considered gesture types

when testing Zipf's law of abbreviation and L , and gesture tokens when testing Menzerath's law and M . Gesture types were defined as gestures which had distinct meaning, occurred repeatedly in the same form of movement and were used singly or in sequence [32]. We considered single gestures to represent a sequence of length one, following earlier work [4,18]; longer gesture sequences were defined as two or more discrete gestures, with <1s between them [25].

d) Analysis

Do chimpanzee play gesture types follow Zipf's law of abbreviation?

We used two-tailed Spearman's rank correlation (IBM SPSS v 22.0) to determine whether mean duration and frequency of use of gestures types were negatively correlated. Mean duration for each gesture type was calculated as $d = D/f$, where D is the sum of all the durations of a particular type and f is the frequency of use of that type (i.e. the number of times the gesture occurred in our dataset) [33].

Emergence of patterns consistent with Zipf's law of abbreviation in correlation analyses such as these could be an artefact of using mean values of signal (here, gesture) duration. Specifically, a negative correlation between two variables, $d = D/f$ and another f , may be inevitable, given d is defined as a quotient involving f , because then $d \approx 1/f$ [34]. This explanation can be rejected if it can be shown that D and f are significantly correlated [33]. For all analyses related to Zipf's law of abbreviation, therefore, we tested for such relationships between D and f , using Spearman's rank correlation.

In addition to testing Zipf's law of abbreviation in the overall gesture repertoire, we conducted further analyses to test for patterns consistent with the law in specific subsets of the repertoire. These analyses were carried out as previous studies and theoretical arguments

indicate this law may be found in parts of a signal repertoire despite not being revealed by analysis of the whole repertoire [13]. For example, in a range of bat species, patterns consistent with the law only emerged when a specific subset of the vocal repertoire – social calls – was considered [14]. In common marmosets, the law was not found in analyses of the entire vocal repertoire [35] but was subsequently found in a subset of the repertoire characterised by low total duration, i.e. calls with low D [13]. In addition to these empirical studies, theoretical arguments suggest that patterns consistent with Zipf’s law of abbreviation may not emerge if pressure for compression is outweighed by other pressures, for example the need to maximise transmission success and/or reach distant receivers, which are predicted to drive an increase in signal magnitude [3]; such pressures may apply to some signals in the repertoire, but not others.

We therefore conducted four further analyses, informed by previous empirical and/or theoretical work, to test Zipf’s law of abbreviation in subsets of the chimpanzee play gestural repertoire. The first divided the repertoire based on values of D , following the general approach of [13] and based on their findings that the law can emerge in low- D but not high- D subsets of the repertoire. The second divided the repertoire based on the frequency of use of gesture types, f , as frequency – or an ordering by frequency – is a fundamental predictor of length in the context of optimal coding according to standard information theory [22,36], while in natural communication systems, compression may act differentially on signals, according to how commonly (or not) they are produced. The third divided the repertoire based on the mean duration of gesture types, d , due to the association between f and d in the context of optimal coding and also for completeness, as $D = fd$. The final analysis divided the repertoire based on the nature of production of gesture types – simple limb and head movements, known as ‘manual gestures’, or movements involving the the whole body, known as ‘whole body signals’ [37] – as it has been proposed that signals that are of greater magnitude (as is the case for whole body signals) may be less likely to reveal patterns consistent with compression [3].

Testing Zipf's law of abbreviation in subsets of the repertoire based on values of D

For these analyses, we adapted the methodology of [13]. In that study, arrangement of signals in order of magnitude of D revealed an obvious breakpoint, demarcating a split between a 'high- D ' cluster and a 'low- D ' cluster. No clear breakpoint was seen in our data (ESM, S2), so we could not conduct a similar analysis to that of [13]. We therefore adopted an alternative approach, with gesture types first listed in ascending order of D , and subsets then created, starting from either the lowest value of D up to the highest value of D , or the reverse procedure (i.e. from highest to lowest D). So for example, the subsets starting from the lowest D contain: (i) the gesture type with the lowest D , (ii) the two gesture types with the lowest and 2nd lowest D (lviii) the 58 gesture types with the lowest, 2nd lowest...58th lowest D (i.e. all gesture types). For all subsets with $n > 4$, we used Spearman's rank correlation to explore the relationship between d and f .

Finally, we investigated whether the pattern of results produced by such a partitioning provided evidence for compression, or rather was an artefact of the sorting by D , using permutation tests implemented in R (v 3.2.3) (for rationale, method and R code, see ESM, S3).

Testing Zipf's law of abbreviation in subsets of the repertoire based on f , and based on d

We followed the methodology described above for D , to create and analyse subsets based on f , and based on d . As before, we used permutation tests to test whether the pattern of results produced by partitionings provided evidence for compression, or rather could be artefactual.

Testing Zipf's law of abbreviation in subsets of the repertoire based on the nature of gestures

We used Spearman's rank correlation to test Zipf's law of abbreviation in manual gestures (n=44 types; ESM, S4), and whole body signals (n=14 types; ESM, S4).

Is the mean duration of chimpanzee play gesture types significantly small?

We first calculated mean duration (L) of gestures types, as defined as in Equation 1 (following [2]), where n is the number of elements within the repertoire, p_i is the normalized frequency of the i -th most likely element and e_i is the magnitude of that element [3]. The normalized frequency of a gesture type was estimated by dividing its frequency by the total frequency of all gesture types. The magnitude of a gesture type was estimated by its mean duration (s).

$$L = \sum_{i=1}^n p_i e_i \quad (1)$$

We then used a permutation test executed in R (for R code, see ESM, S5A) to test whether L was significantly small [38]. A control of L (L') was defined over the permutation function $\pi(i)$, as shown in Equation 2 [3]. The left p -value was computed by Q_L/Q , with Q_L being the number of uniformly random permutations where $L' \leq L$, and Q the total number of permutations ($=10^5$). The right p -value was computed by Q_R/Q , with Q_R being the number of random permutations where $L' \geq L$, and Q the total number of permutations ($=10^5$).

$$L' = \sum_{i=1}^n p_i e_{\pi(i)} \quad (2)$$

Do chimpanzee play gesture sequences follow Menzerath's law?

We used Spearman's rank correlation to determine whether sequence size (number of gestures) and mean gesture duration were negatively correlated. It is a moot point whether

single signals should be counted as sequences (i.e. of size 1), so analyses were run both for the complete dataset (i.e. sequences of all sizes, including single gestures) and for a dataset excluding single gestures (i.e. sequences of two or more gestures).

In the context of Menzerath's law in chimpanzee gestures, D is defined as the total duration of gestures in a sequence (excluding durations of gaps between consecutive gestures), d as the mean duration of gestures and n as the number of gestures in that sequence. Menzerath's law holds if there is a significant negative correlation between $d=D/n$ and n . It has been argued that patterns consistent with Menzerath's law could emerge as an inevitable consequence of exploring the relationship between variables such as n and $d=D/n$ because d would scale with n automatically as $d \approx 1/n$ [34]. However, rigorous mathematical analysis has shown that this can only happen in a very special condition, namely when D is mean independent of n , a property that can be tested with a simple test of the correlation between D and n [39]. To exclude this simplistic explanation for the finding of Menzerath's law, a further analysis was done [39,40], following methods used to explore the robustness of results relating to Menzerath's law in genomes [41]. To test whether Menzerath's law in chimpanzee gestural sequences is an inevitable consequence of trivial scaling, we used Spearman's rank correlation to test the relationship between D and n ; a significant negative relationship excludes the trivial explanation.

Is the expected total sum of the duration of gestures of each sequence significantly small?

The total duration of a collection of sequences is defined as

$$M = \sum_{i=1}^T D_i, \quad (3)$$

where D_i is the total duration of the i -th sequence.

In turn,

$$D_i = \sum_{j=1}^{n_i} l_{ij}, \quad (4)$$

where n_i is the number of elements of the i -th sequence and l_{ij} is the duration of the j -th element of the i -th sequence. Defining the mean duration of the i -th sequence as $\langle l_{ij} \rangle_i = D_i/n_i$, M can be expressed as

$$M = \sum_{i=1}^T n_i \langle l_{ij} \rangle_i. \quad (5)$$

To test whether the total sum of the duration of gestures of each sequence is significantly small, we calculated M following Equation 5. The calculation of M is defined over a summation of tokens, with each occurrence of a sequence considered an individual token. We used a similar permutation test as for the testing of significance of L , executed in R (for R code, see ESM, S5B), to check whether M was significantly small [3]. n_i has the role of p_i and $\langle l_{ij} \rangle_i$ has the role of e_i in the test. Namely, n_i and $\langle l_{ij} \rangle_i$ remain constant during the test.

Results

Durations of 2137 play gestures were measured; these comprised 58 gesture types, given by 48 individual chimpanzees. Of these 2137 gestures, 873 occurred as single gestures and the remaining 1264 in sequences ranging from 2-45 gestures (Table 1). Infants produced 492 (23.02%) of gestures, juveniles 940 (43.99%), subadults 638 (29.85%) and adults 67 (3.14%) (ESM, S4).

Do play gestures follow Zipf's law of abbreviation?

Testing Zipf's law of abbreviation in the overall repertoire

There was no significant correlation between mean duration (d) and frequency of use, (f) of gesture types ($r_s = -0.005$, $n=58$, $p=0.97$, Figure 1). The mean duration of gesture types (L) was 2.65s; this was not significantly small ($n= 58$, $p=0.42$).

Testing Zipf's law of abbreviation in subsets of the repertoire based on values of D

Zipf's law of abbreviation was prevalent in subsets of gesture types with low- D (Figure 2a; for full results, see ESM, S6). Considering successive subsets of gesture types generated from low- D to high- D (with $n>4$), a significant negative correlation between d and f was first seen in the subset comprising gestures with the five lowest D values; as gesture types with higher D -values were added in one at a time, the correlation between d and f remained significant until the subset of gesture types with the 41 lowest D values, after which p values fluctuated around 0.05 until the subset with the 48 lowest D values, from which point all correlations were nonsignificant. L was significantly small for all subsets of gesture types generated from low- D to high- D , up to that of gesture types with the 55 lowest values of D (ESM, S6). D and f were significantly correlated – and thus agreement with Zipf's law of abbreviation does not appear to be an artefact of analysing mean gesture duration – for the subset containing the gesture types with the 9 lowest values of D and for all larger subsets (ESM, S6). In addition, the permutations tests provided evidence for compression across a wide range of subsets of gesture types with lowest values of D (ESM, S3).

The pattern of results in subsets generated in the opposite direction – from high- D to low- D – was somewhat different (Figure 2a; for full results, see ESM, S6). A significant negative correlation between d and f was not seen until the subset containing the 15 gesture types with the highest D values; the correlation remained significant until the subset containing the 35 gestures types of highest D and then – with the exception of the subset containing the 38

gesture types of highest D – was nonsignificant in all other, increasingly large, subsets. L was significantly small from the subset containing the 21 gesture types of highest D up to the subset with the 38 gesture types of highest D (ESM, S6). While D and f were significantly correlated for the subsets containing the gestures with the 10, 11, 13, 14, and 20 highest values of D and for all subsets larger than this (ESM, S6), importantly the permutation tests did not provide evidence for compression in subsets of gesture types with high values of D , indicating significant correlations in these subsets are an artefact of the sorting process (ESM, S3).

Testing Zipf's law of abbreviation in subsets of the repertoire based on values of f

When gestures were grouped in order of f , significant negative relationships between d and f were found only in a small number of subsets and the permutation tests did not provide evidence for compression (Figure 2b; for full results, and calculations of L and the correlations between D and f , see ESM, S7; for results of the permutation tests see ESM, S3).

Testing Zipf's law of abbreviation in subsets of the repertoire based on values of d

Analysis of subsets of gestures grouped according to d revealed only a few significant negative relationships between d and f . The permutation tests provided evidence for compression in a narrow range of the subsets of gesture types with highest values of d , but not elsewhere (Figure 2c; for full results, and for calculations of L and the correlations between D and f , see ESM, S8; for results of the permutation tests see ESM, S3).

Testing Zipf's law of abbreviation in subsets of the repertoire based on nature of gestures

Analysis of manual gestures revealed no relationship between d and f ($r_s = -0.125$, $n = 44$, $p = 0.419$) and L was not significantly small (2.09s, $p = 0.148$). Unexpectedly, whole body signals showed a significant positive relationship between d and f ($r_s = 0.746$, $n = 14$, $p = 0.002$) –

the opposite pattern to that predicted by Zipf's law of abbreviation – and L was significantly large (5.29s, $p < 0.0001$).

Do chimpanzee play gesture sequences follow Menzerath's law?

There was a significant negative correlation between sequence size (n_i) and mean constituent gesture duration ($\langle l_{ij} \rangle_i$), both when including single gestures ($r_s = -0.077$, $n = 1313$, $p = 0.006$ – Figure 3), and when excluding single gestures ($r_s = -0.156$, $n = 440$, $p = 0.001$). These relationships remained significant after removing the outlying data point – a sequence including 45 gestures (including single gestures: $r_s = -0.074$, $n = 1312$, $p = 0.007$; excluding single gestures: $r_s = -0.149$, $n = 439$, $p = 0.002$).

There was a significant positive correlation between sequence size (n_i) and the total constituent gesture duration (D_i) (including single gestures – $r_s = 0.403$, $n = 1313$ and $p < 0.0001$; excluding single gestures – $r_s = 0.209$, $n = 440$ and $p < 0.0001$), confirming that the finding of Menzerath's law was not an artefact of inevitable, trivial scaling.

The total sum of the duration of gestures of each sequence, M , was 5653.82s in the complete dataset and 3050.06s in the dataset excluding single gestures; both values of M were significantly small (including single gestures : $n = 1313$, $p < 0.0001$; excluding single gestures: $n = 440$, $p < 0.0001$).

Discussion

We tested for evidence of compression in chimpanzee play gestural communication, firstly by investigating whether gesture types and gesture sequences follow linguistic laws that reflect this principle, and secondly by testing whether measures of mean code length of types and sequences are significantly small. Individual gesture types were initially found not to follow Zipf's law of abbreviation (which predicts a negative relationship between signal length

and frequency of use); however, subsequent analyses of specific subsets of the overall gestural repertoire did reveal strong agreement with this law, and also evidence that mean code length – here, gesture duration – was significantly small. Unexpectedly, patterns opposite to the law were found in one subset of gestures, whole body signals. Sequences of gestures followed Menzerath’s law (according to which longer sequences are made up of shorter constituents), and again mean code length – here the total sum of the duration of gestures – was significantly small. These findings indicate that compression has shaped chimpanzee play gestural communication at two levels of organisation – the pattern of use of individual gesture types, and the construction of gesture sequences. Our results extend the evidence for compression in animal communication for the first time to the gestural mode of signalling; in conjunction with findings from studies of non-vocal behaviour in dolphins [15], a range of animal vocal systems [3–5,14,18], human speech [42] written texts [9,10] and sign language [12], this work provides additional support for the hypothesis that compression is a general principle underpinning diverse forms and modalities of communication.

Such a hypothesis is supported by strong predictions of information theory in relation to three linguistic laws. Concerning Zipf’s law of abbreviation, these predictions have in common that optimal coding of information (minimum L) implies that the correlation between the relative frequency of a type, p , and its length l , cannot be positive [22]. Standard information theory is able to predict the actual relationship between length and frequency in case of a fully optimized system. In the case of optimal, uniquely decipherable encoding, l should approximate $-\log p$ [36]. In the case of optimal non-singular encoding, the length of a type of frequency rank i (the most frequent type has rank 1) should approximate $\log i$ [22]. These arguments have been extended to predict Menzerath’s law from optimal coding (minimum M) [4]. Finally, the well studied and ubiquitous Zipf’s law for word frequencies may also be a consequence of compression [43]. Support for such a powerful and abstract

mechanism comes from the ubiquity of the law of abbreviation in human language, independent of modality (speech vs signed) [12,42] or writing system (character-based vs letter-based) [6,9,10].

Results from our analyses of Zipf's law of abbreviation reiterate a key point raised by previous studies [13,14], namely that exploration of linguistic laws in non-human systems may require investigation of patterns at levels below the complete repertoire of signals. Overall, individual play gesture types of chimpanzees did not conform to the pattern predicted by this law; however, very strong agreement was seen in subsets of the repertoire, particularly those for which D , the product of mean duration (d) and frequency of use (f), was small. By contrast, analyses of subsets based on d and f revealed little agreement with Zipf's law of abbreviation. D can be viewed as a 'total cost' function, and it may appear counterintuitive that it is gestures that have low total cost in which compression appears most prevalent; greater savings in terms of coding efficiency could, in principle, be gained among gestures with high total cost. However, it is possible that low D gestures are low D precisely because of compression; this principle may have acted to improve coding efficiency not only by aligning frequency of use and duration of such gestures, but also by reducing these two measures (and hence their product) overall.

Alternatively, there may be reasons why among other gestures, patterns consistent with compression are not found. One possibility is that compression does not affect such gestures, contrary to the recent proposal that compression is a universal principle underpinning not just animal behaviour [3], but biological information systems in the broadest sense [4]. Indeed, pressure for efficiency may be reduced in the context we explored – social play – as this behaviour is associated with having excess time and/or energy [44]. However, a lack of agreement with Zipf's law of abbreviation does not preclude that compression acts in a system. Universal principles do not necessarily produce universal patterns. Even when a principle

holds, other forces may drive the emergence of patterns that are, superficially, inconsistent with those predicted by the principle alone [3]; this situation appears recurrently in optimization models of communication [45,46]. The challenge is to identify what such forces might be, and to explore under which circumstances they outweigh the underlying principle [3]

Compression is the minimization of redundancy in a system, and absence of a pattern predicted by this principle among a set of chimpanzee play gestures (and the repertoire overall) may be due to redundancy being added in parts of the repertoire. Coding theory indicates that building redundancy into signals – for example by elongating them – reduces the risk of transmission errors [36]. In our study system, such errors could be costly as social play can become rough and may, in extreme cases, lead to aggressive escalations [47]. Regulatory gesture types used during play (e.g. *head stand*, *dangle*, *roll over*) or which signal play stop or change (e.g. *hand on*), may therefore need to be used very explicitly to ensure continued peaceful play [32]; notably, these gesture types tend to be characterised by high D . The cost of adding redundancy to certain gestures (increasing their duration) may therefore be outweighed by the cost of aggression resulting from a signal being misinterpreted.

Grouping gestures by their frequency of occurrence, f , did not produce clear patterns of agreement with Zipf's law of abbreviation. This outcome is surprising, as a number of results from standard information theory link the frequency of a type, f , with its length in the context of optimal coding. For example, the length of a type whose relative frequency is p should approximate $-\log p$ in the case of optimal uniquely decipherable encoding [36]; and the length of a type of frequency rank i (the most frequent type has rank 1) should approximate $\log i$ in the case of optimal non-singular coding [22]. These results indicate that frequency, or an ordering induced by frequency, is fundamental for standard information theory and thus we might expect this to be the case for animal communication.

However, our results suggest that D captures the pressure for optimization much better than f in this real-world biological system. An intriguing possible explanation for this is that conclusions of standard information theory cannot be extrapolated completely to such systems, for example because the assumptions of the theory may not be valid. Standard information theory provides a one-way approach to optimal coding: it provides the minimum lengths of the string of each type given the probability of the types. Thus, the length of a type is caused by its frequency, not *vice versa*. However, type frequencies vary in natural communication systems and therefore within these systems there may be pressures reflecting a two-way solution to optimal coding: type frequency may influence its string length (as in standard information theory) and *vice versa* – the string length of a type may influence its frequency. In a two-way optimization system, natural selection would operate on the product of frequency and duration, not on duration or frequency alone.

Analyses of gestures grouped by mean duration, d , also revealed little agreement with Zipf's law of abbreviation. The poor performance of d in detecting agreement with this law is not surprising as information theory predicts a strong correlation between d and f (or between d and the frequency rank), and if f has failed to partition the repertoire in a way that reveals agreement with Zipf's law abbreviation, the same should apply to d . Our results for subsets grouped by d , in conjunction with those grouped by f , indicate that it is not among calls that are on average short, or those that are rarely given, that compression is most evident, but rather among calls where both things are the case (the product of f and d is D).

Analyses of Zipf's law of abbreviation in manual gestures and in whole body signals revealed no evidence for the law in the former, but a pattern opposite to that predicted by the law in the latter. While some previous studies of animal communication have found a lack of support for this law [3], to our knowledge this is the first time that a significant positive relationship has been found – in non-human or human communication – between signal

duration and frequency of use. This result provides compelling evidence to refute proposals [34] that patterns consistent with linguistic laws are inevitable, and thus that such laws are scientifically trivial. A pattern opposite to that predicted by Zipf's law of abbreviation may arise via a number of routes: redundancy may have been added in a positive relationship with frequency of use i.e. more common whole body signals include the greater degree of redundancy; compression may act in positive relationship to rarity i.e. more rarely used whole body signals are more compressed; or both pressures may be at work. A key factor to consider with respect to whole body signals is that some require a posture to be held in place to be clearly identified as a specific signal; for example, a *head stand* is only clearly a *head stand*, and not half a *somersault* or some other movement, because the signaller stops in the unusual position of standing with their head between their feet and holds that position. This unavoidable extension of certain signals – potentially in conjunction with an absence or relaxation of energetic constraints [44] – may underlie the positive association between whole body signal duration and frequency of use.

Our finding that chimpanzee play gestural sequences follow Menzerath's law, a linguistic law first derived from studies of human language and recently shown also to apply to vocal sequences of geladas [4] and chimpanzees [18], suggests that comparable principles of self-organization [48] underpin these different combinatorial communication systems. This law has not previously been explored in gestural communication in humans or other species; our results provide new evidence of an important commonality between human language and primate gestural communication, with respect to the basic structural patterns underpinning how signals are combined into larger structures. In studies of this law in primate vocal communication [4,18], breathing-related constraints and energetic demands of vocal production were implicated as important drivers of the negative relationship between the number of calls in a sequence and their mean duration. Gestural sequences are not constrained

by breathing patterns, as is the case for vocal sequences. Energetic constraints, associated with the increased muscular activity involved in producing gestures, and especially prolonged gesture bouts [49], may underlie the emergence of Menzerath's law in this system.

Our work adds to a growing literature in which statistical laws derived from studies of human language are found to hold in non-human systems [3–5,14,15,18]. Identifying shared common properties of language and other natural systems, and examining the mathematical underpinning of such properties, not only provides new insights into the fundamental principles of natural organisation [3], but also presents an important opportunity to explore the evolutionary history of universal linguistic patterns [4]. Many linguistic laws remain to be explored beyond our own species; we hope our work will encourage such investigations across diverse biological information systems.

Ethics. Permission for data collection was provided by the University of St Andrews Animal Welfare and Ethics Committee.

Data, code and materials. R codes supporting this article are in ESM. Datasets are published on figshare.com (<https://doi.org/10.6084/m9.figshare.5970823.v1>).

Competing interests. We declare no competing interests.

Author contributions. RH and SS conceived the study; RH, SS and RFC designed the study; CH provided the raw data (video recordings and gesture classification); RH and RFC analysed data; RH and SS wrote the paper, with editing by RFC and CH. All authors gave final approval for publication.

Acknowledgements. We thank Dr Peter Shaw for statistical advice, Dr Emilie Genty for advice on classification of whole body signals and manual gestures, Uganda National Council for Science and Technology and Uganda Wildlife Authority for permission to collect the data, and the Royal Zoological Society of Scotland and Budongo Conservation Field Station staff for invaluable support. We thank Dr David Leavens for facilitating this collaboration, and two anonymous reviewers for their thoughtful comments and feedback. We also thank Argimiro Arratia for advice on R.

Funding. RFC is funded by grants 2014SGR 890 (MACDA) from AGAUR (Generalitat de Catalunya) and the grant Management and Analysis of Complex Data (TIN2017-89244-R) from MINECO (Ministerio Economía Industria y Competitividad). Fieldwork of CH was generously supported by grants from Wenner-Gren Foundation and Russell Trust. SS thanks Santander for a Research and Travel grant used to work on this study. RH thanks Kölner Gymnasial- und Stiftungsfonds for financial support.

References

1. Köhler R, Altmann G, Piotrowski RG. 2005 *Quantitative linguistics – an international handbook*. Berlin / New York: Walter de Gruyter.
2. Altmann EG, Gerlach M. 2016 Statistical laws in linguistics. pp. 7–26. Springer, Cham. (doi:10.1007/978-3-319-24403-7_2)
3. Ferrer-i-Cancho R, Hernández-Fernández A, Lusseau D, Agoramoorthy G, Hsu MJ, Semple S. 2013 Compression as a universal principle of animal behavior. *Cogn. Sci.* **37**, 1565–1578. (doi:10.1111/cogs.12061)
4. Gustison ML, Semple S, Ferrer-i-Cancho R, Bergman TJ. 2016 Gelada vocal

- sequences follow Menzerath's linguistic law. *Proc. Natl. Acad. Sci.* **113**, E2750–E2758. (doi:10.1073/pnas.1522072113)
5. Semple S, Hsu MJ, Agoramoorthy G. 2010 Efficiency of coding in macaque vocal communication. *Biol. Lett.* **6**, 469–471. (doi:10.1098/rsbl.2009.1062)
 6. Zipf G. 1936 *The psycho-biology of language: an introduction to dynamic philology*. London, UK: George Routledge and Sons Ltd.
 7. Zipf G. 1949 *Human behaviour and the principle of least effort*. Cambridge: MA: Addison Wesley.
 8. Bentz C, Ferrer-i-Cancho R. 2015 Zipf's law of abbreviation as a language universal. Capturing Phylogenetic Algorithms for Linguistics. In *Lorentz Center Workshop*,
 9. Wang Y, Chen X. 2015 Structural complexity of simplified chinese characters. In *Recent contributions to quantitative linguistics* (eds A Tuzzi, M Benešová, J Macutek), pp. 229–240. Berlin/Boston: Walter de Gruyter.
 10. Sanada H. 2008 *Investigations in Japanese historical lexicology*. Göttingen: Peust & Gutschmidt.
 11. Hernández-Fernández A, Casas B, Ferrer-i-Cancho R, Baixeries J. 2016 Testing the Robustness of Laws of Polysemy and Brevity Versus Frequency. pp. 19–29. Springer, Cham. (doi:10.1007/978-3-319-45925-7_2)
 12. Börstell C, Hörberg T, Östling R. 2016 Distribution and duration of signs and parts of speech in Swedish Sign Language. *Sign Lang. Linguist.* **19**, 143–196. (doi:10.1075/sll.19.2.01bor)
 13. Ferrer-i-Cancho R, Hernández-Fernández A. 2013 The failure of the law of brevity in two New World primates. Statistical caveats. *Glottology* **4**, 44–55.

14. Luo B, Jiang T, Liu Y, Wang J, Lin A, Wei X, Feng J. 2013 Brevity is prevalent in bat short-range communication. *J. Comp. Physiol. A* **199**, 325–333. (doi:10.1007/s00359-013-0793-y)
15. Ferrer-i-Cancho R, Lusseau D. 2009 Efficient coding in dolphin surface behavioral patterns. *Complexity* **14**, 23–25. (doi:10.1002/cplx.20266)
16. Altmann G. 1980 Prolegomena to Menzerath's law. *Glottometrika* **2**, 1–10.
17. Teupenhayn R, Altmann G. 1984 Clause length and Menzerath's law. *Glottometrika* **6**, 127–138.
18. Fedurek P, Zuberbühler K, Semple S. 2017 Trade-offs in the production of animal vocal sequences: insights from the structure of wild chimpanzee pant hoots. *Front. Zool.* **14**, 50. (doi:10.1186/s12983-017-0235-8)
19. Ferrer-i-Cancho R, Forns N. 2010 The self-organization of genomes. *Complexity* **15**, 34–36. (doi:10.1002/cplx.20296)
20. Li W. 2012 Menzerath's law at the gene-exon level in the human genome. *Complexity* **17**, 49–53. (doi:10.1002/cplx.20398)
21. Shahzad K, Mittenthal JE, Caetano-Anollés G. 2015 The organization of domains in proteins obeys Menzerath-Altmann's law of language. *BMC Syst. Biol.* **9**, 44. (doi:10.1186/s12918-015-0192-9)
22. Ferrer-i-Cancho R, Bentz C, Seguin C. 2015 Compression and the origins of Zipf's law of abbreviation. *arXiv:1504.04884* (doi:arXiv:1504.04884)
23. Arbib MA, Liebal K, Pika S. 2008 Primate vocalization, gesture, and the evolution of human language. *Curr. Anthropol.* **49**, 1053–1076. (doi:10.1086/593015)

24. Call J, Tomasello M. 2007 *The gestural communication of apes and monkeys*. New Jersey: Lawrence Erlbaum Associates.
25. Hobaiter C, Byrne RW. 2011 Serial gesturing by wild chimpanzees: its nature and function for communication. *Anim. Cogn.* **14**, 827–838. (doi:10.1007/s10071-011-0416-3)
26. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. (doi:10.1163/156853974X00534)
27. Hayaki H. 1985 Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* **26**, 343–360. (doi:10.1007/BF02382452)
28. Hobaiter C, Byrne RW. 2011 The gestural repertoire of the wild chimpanzee. *Anim. Cogn.* **14**, 745–767. (doi:10.1007/s10071-011-0409-2)
29. Landers RN. 2015 Computing intraclass correlations (ICC) as estimates of interrater reliability in SPSS. *The Winnower* **2**, e143518. (doi:10.15200/winn.143518.81744)
30. Brainerd B. 1972 On the relation between types and tokens in literary text. *J. Appl. Probab.* **9**, 507–518. (doi:10.1017/S002190020003583X)
31. Wetzel L. 2011 Types and tokens. In *The Stanford Encyclopedia of Philosophy* (ed E Zalta),
32. Hobaiter C, Byrne RW. 2014 The meanings of chimpanzee gestures. *Curr. Biol.* **24**, 1596–1600. (doi:10.1016/j.cub.2014.05.066)
33. Semple S, Hsu MJ, Agoramoorthy G, Ferrer-i-Cancho R. 2013 The law of brevity in macaque vocal communication is not an artefact of analysing mean call durations. *J. Quant. Linguist.* **20**, 209–217. (doi:10.1080/09296174.2013.799917)

34. Solé R V. 2010 Genome size, self-organization and DNA's dark matter. *Complexity* **16**, 20–23. (doi:10.1002/cplx.20326)
35. Bezerra BM, Souto AS, Radford AN, Jones G. 2011 Brevity is not always a virtue in primate communication. *Biol. Lett.* **7**, 23–25. (doi:10.1098/rsbl.2010.0455)
36. Cover T, Thomas J. 2006 *Elements of information theory*. New York: Wiley.
37. Genty E, Clay Z, Hobaiter C, Zuberbühler K. 2014 Multi-modal use of a socially directed call in bonobos. *PLoS One* **9**, e84738. (doi:https://doi.org/10.1371/journal.pone.0084738)
38. Sokal RR, Rohlf FJ. 1995 *Biometry: the principles and practice of statistics in biological research*. New York: W.H. Freeman & Co.
39. Ferrer-i-Cancho R, Hernández-Fernández A, Baixeries J, Dębowski L, Mačutek J. 2014 When is Menzerath-Altmann law mathematically trivial? A new approach. *Stat. Appl. Genet. Mol. Biol.* **13**, 633–644. (doi:10.1515/sagmb-2013-0034)
40. Ferrer-i-Cancho R, Forns N, Hernández-Fernández A, Bel-Enguix G, Baixeries J. 2013 The challenges of statistical patterns of language: The case of Menzerath's law in genomes. *Complexity* **18**, 11–17. (doi:10.1002/cplx.21429)
41. Hernández-Fernández A, Baixeries J, Forns N, Ferrer-i-Cancho R. 2011 Size of the whole versus number of parts in genomes. *Entropy* **13**, 1465–1480. (doi:10.3390/e13081465)
42. Ridley DR. 1982 Zipf's Law in transcribed speech. *Psychol. Res.* **44**, 97–103. (doi:10.1007/BF00308559)
43. Ferrer-i-Cancho R. 2016 Compression and the origins of Zipf's law for word frequencies. *Complexity* **21**, 409–411. (doi:10.1002/cplx.21820)

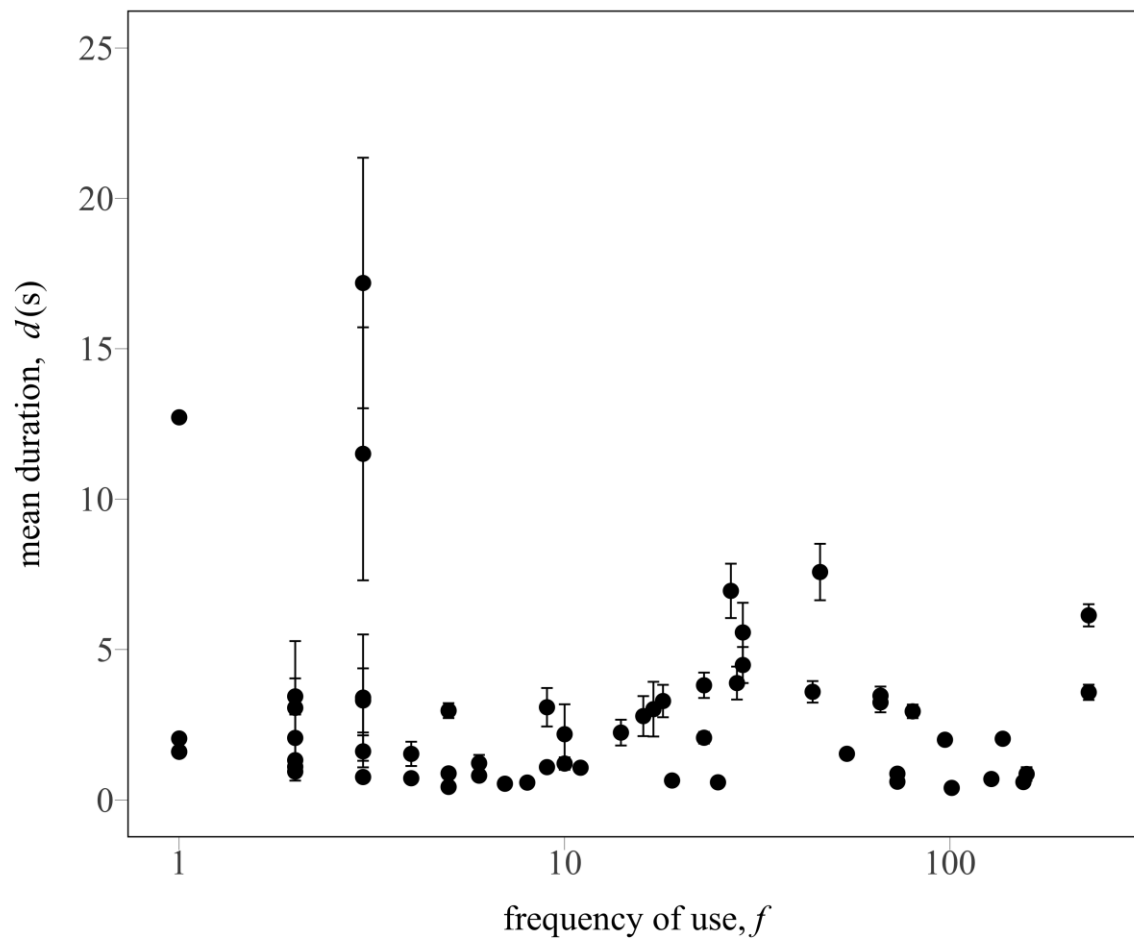
44. Held SDE, Špinka M. 2011 Animal play and animal welfare. *Anim. Behav.* **81**, 891–899. (doi:10.1016/j.anbehav.2011.01.007)
45. Ferrer-i-Cancho R. 2017 The placement of the head that maximizes predictability. An information theoretic approach. *Glottometrics* , 38–71.
46. Ferrer-i-Cancho R. 2005 Zipf's law from a communicative phase transition. *Eur. Phys. J. B - Condens. Matter Complex Syst.* **47**, 449–457. (doi:10.1140/epjb/e2005-00340-y)
47. Pellis SM, Pellis VC. 1996 On knowing it's only play: The role of play signals in play fighting. *Aggress. Violent Behav.* **1**, 249–268. (doi:10.1016/1359-1789(95)00016-X)
48. Köhler R. 1987 System theoretical linguistics. *Theor. Linguist.* **14**, 241–258. (doi:10.1515/thli.1987.14.2-3.241)
49. Scott CB. 2008 *A primer for the exercise and nutrition sciences: thermodynamics, bioenergetics, metabolism*. Humana Press. (doi:https://doi.org/10.1007/978-1-60327-383-1)

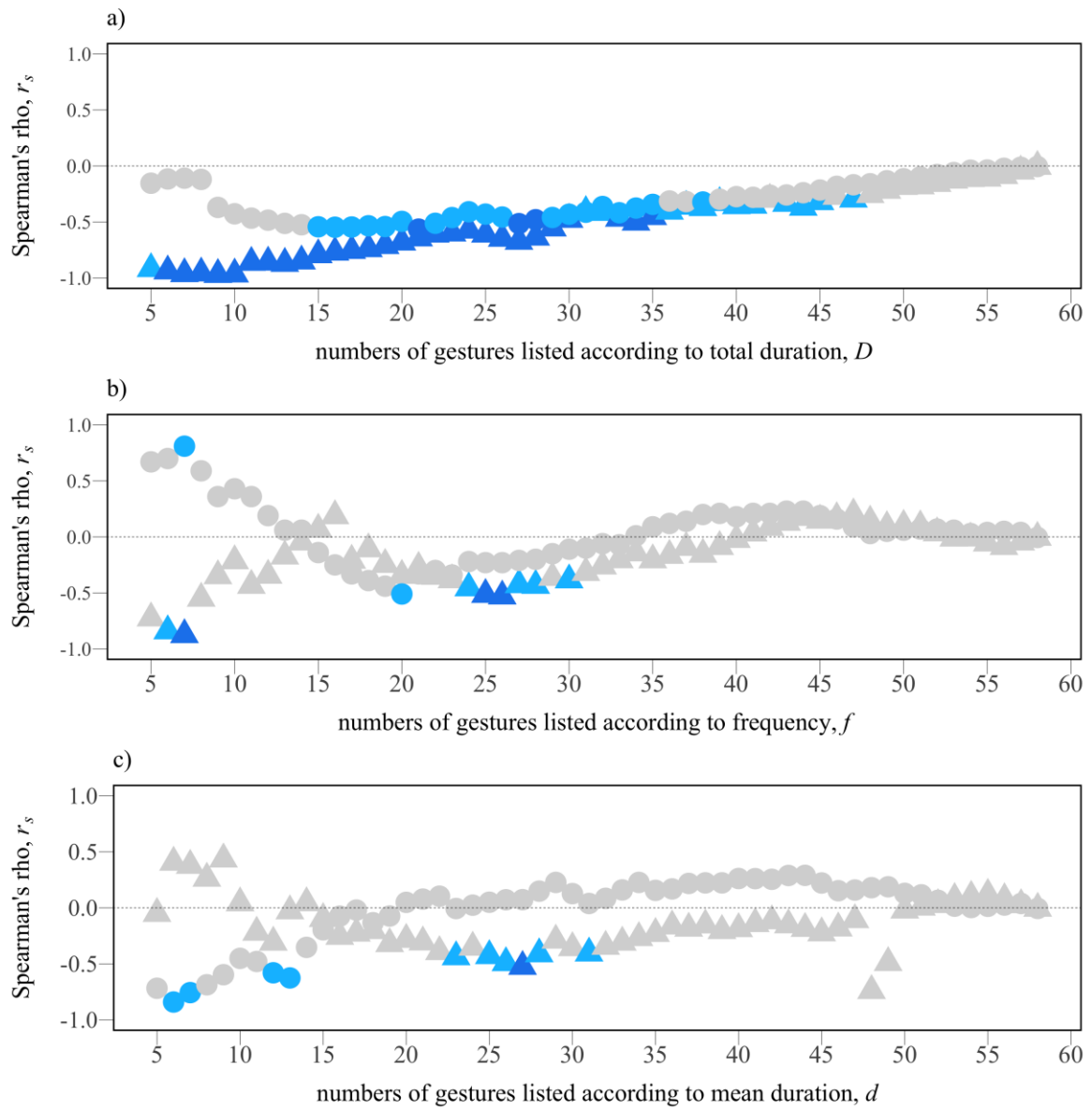
Figure legends

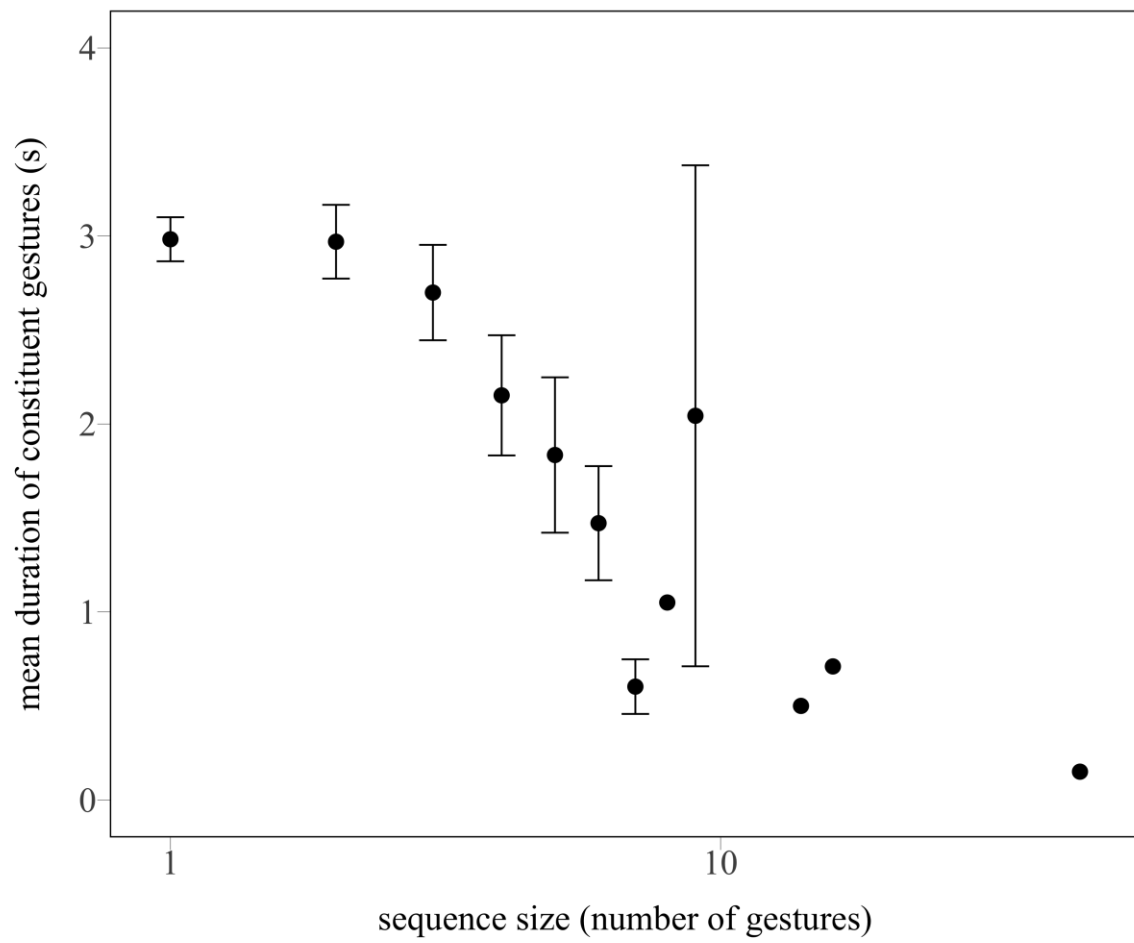
- Figure 1** Relationship between mean duration (d) and frequency of use (f) of gesture types. The x -axis is displayed in log scale. Whiskers indicate S.E.M. Lack of whiskers indicates either small variation of durations within a gesture type or that a gesture type was only used once.
- Figure 2** Coefficients of correlation (Spearman's rank correlation) between mean duration (d) and frequency of use (f) of gesture types, for the subsets of gesture types generated either by incrementally including gesture types from lowest to highest (triangles) or highest to lowest (circles) values of a) D , b) f and c) d . Symbols in grey indicate $p > 0.05$, in light blue indicate $p < 0.05$ but > 0.01 , and in dark blue indicate $p < 0.01$.
- Figure 3** Relationship between mean constituent gesture duration and sequence size in terms of number of gestures in play gesture sequences. The x -axis is displayed in log scale. Whiskers indicate S.E.M. Lack of whiskers indicates that a sequence of this size was only used once.

Table 1 Frequency, n , of gesture sequences according to their size (number of gestures in the sequence).

Table 1	
Sequence size	n
1	873
2	267
3	93
4	42
5	17
6	10
7	4
8	1
9	3
14	1
16	1
45	1

**Figure 1**

**Figure 2**

**Figure 3**

Electronic Supplementary Material**S1****Play gesture ethogram**

Gesture type descriptions after [1]

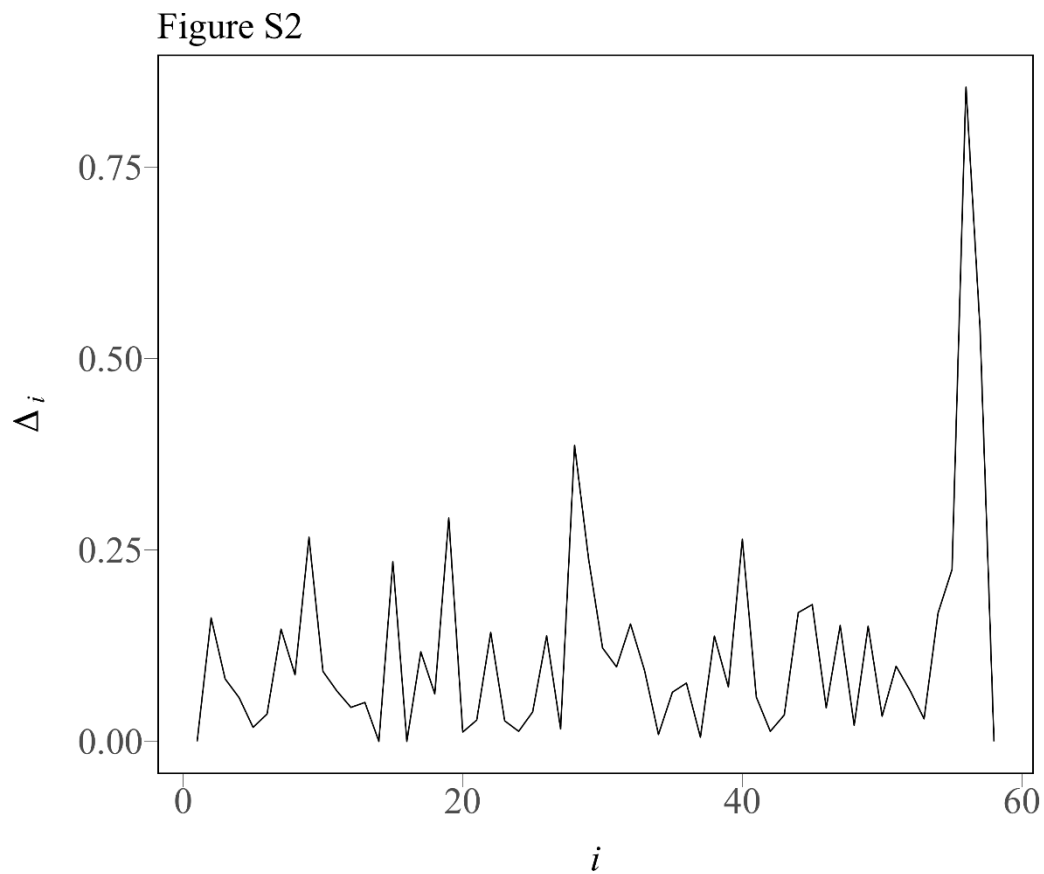
Gesture type	Description
Arm raise	Raise arm and/or hand vertically in the air
Arm shake	Small repeated back and forth motion of the arm
Arm swing	Large back and forth movement of the arm held below the shoulder (individual can hold an object)
Arm wave	Large repeated back and forth movement of the arm (s) raised above the shoulder
Bite	Part of recipient's body is held between the teeth of the signaller
Bow	Signaller bends forward from the waist while standing
Clap	Both palms moved towards each other and brought together with an audible contact
Dangle	To hang from one or both arms from a branch above another individual, this is audible as there is normally significant disturbance of the canopy
Directed push	A light short non-effective push that indicates a direction of desired movement, immediately followed by the recipient moving as indicated
Drum object (palms)	Short hard audible contact of alternate palms against an object
Drum other	As 'drum object (palms)' but contact is with recipient's body
Embrace	Signaller wraps both arms around the recipient and maintains physical contact
Feet shake	Repeated back and forth movement of feet from the ankles
Grab	The hand or foot is firmly closed over part of the recipient's body; 1- or 2-handed; Individual can hold onto the body of the recipient
Grab-pull	As 'Grab' but closed hand contact is maintained and a force exerted to move the recipient from its current position; 1- or 2-handed
Gallop	An exaggerated running movement where the contact of the hands and feet is deliberately audible
Hand on	Palm or knuckles of the hand is placed on the recipient, contact lasts for more than 2 s
Hand shake	Repeated back and forth movement of hand (s) from the wrist
Head butt	Head is briefly and firmly pushed into the body of the recipient
Head nod	Repeated back and forth movement of the head; head nodding or shaking
Head stand	Signaller bends forward and places head on the ground
Hide face	Face is hidden by the hands and/or arms
Hit with object	An object is brought into short hard contact with the body of the recipient
Jump	While bipedal both feet leave the ground simultaneously, accompanied by horizontal displacement through the air
Kick	Foot is brought into short hard contact with the recipient's body or an object in a movement from the hip with a horizontal element
Knock object	Back of the hand or knuckles are brought into short hard audible contact with an object
Leaf clipping	Strips are torn from a leaf (or leaves) held in the hand using the teeth
Leg swing	Large back and forth movement of the leg from the hip
Look	Signaller holds an eye-contact position with the recipient— minimum duration 2 s
Object in mouth	Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch)
approach	
Object move	Object is displaced in one direction, contact is maintained through movement
Object shake	Repeated back and forth movement of an object; 1- or 2-handed

Gesture type	Description
Pirouette	Signaller turns around their body's vertical axis while also displacing along the ground
Poke	Firm, brief push of one or more fingers into the recipient's body
Pounce	Signaller displaces through the air to land quadrupedally on the body of the recipient
Punch object / ground	Movement of whole arm, with short hard audible contact of closed fist to an object or the ground
Punch other	As 'punch object/ground' but contact is with recipient's body
Push	Palm in contact with recipient's body and force is exerted in attempt to displace recipient
Reach	Arm extended to the recipient with hand in an open, palm upwards position (no contact)
Roll over	The signaller rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs
Side roulade	Body is rotated around the head- feet axis while lying on the ground with horizontal displacement along the ground
Slap object	Movement of the arm from the shoulder with hard short contact of the palm of the hand to an object; 1- or 2-handed
Slap object with object	As 'slap object' but the hand holds an object which is brought into contact with another object (e.g. a branch is slapped against a tree); 1- or 2-handed
Slap other	As 'slap object' but the palm is brought into contact with the recipient's body; 1- or 2-handed
Somersault	Signaller's body is curled into a compact position on the ground, and rolled forwards so the feet are brought over the head and returned to sitting position
Stiff walk	Walk quadrupedally with a slow exaggerated movement
Stomp	Sole of one foot is lifted vertically and brought into a short hard audible contact with the surface being stood upon (e.g. ground or a branch)
Stomp other	As 'stomp' but contact is made with recipient
Stomp 2-feet	As 'stomp single' but both feet used
Stomp 2-feet alternate	As 'stomp 2-feet' but both feet are used alternately (e.g. walking by stomping with feet alternately)
Stomp 2-feet other	As 'stomp 2-feet' but contact is made with recipient
Stomp 2-feet other alternate	As 'stomp 2-feet alternate' but contact is made with recipient
Tandem walk	Subject positions arm over the body of the recipient and both walk forward while maintaining position
Tap object	Movement of the arm from the wrist or elbow, with firm short contact of the fingers to the object
Tap other	As 'tap object' but contact is with recipient's body
Throw object	Object is moved and released so that there is displacement through the air after moment of release
Touch other	Light contact of the palm and/or fingers on the body of the recipient, contact under 2 s
Water splash, 1 hand	Hand is moved vigorously through the water so that there is audible displacement of the water

S2

Differences in magnitude of D (i.e. Δ_i) between the i -th and the $(i-1)$ -th gesture type with the smallest total duration, D .

To identify any potential breakpoint in values of D , we investigated potential cluster boundaries by defining the differences in the orders of magnitude between successive D -values, as $\Delta_i = \log(D_i/D_{i-1})$, where Δ_i is the difference in magnitude between the i -th D value and its consecutive D -value (note, D -values are listed in ascending order). Evidence for a clear breakpoint was explored by plotting Δ_i against i (Figure S2); no such clear breakpoint was seen.



S3

The effect of sorting by f , d or D Rationale and Methods

We explored whether the law of abbreviation emerges when sorting gesture types by D , f or d . We wished to investigate the extent to which any appearance of the law of abbreviation in subsets produced in this way could be merely due to the sorting itself, rather than an effect of compression.

For this reason, we considered the three variables for sorting, i.e. D , f , and d , and two orders, i.e. ascending and descending, which gives six possible configurations. The dataset relevant for the law of abbreviation can be seen as a matrix with two columns, f and d , and gesture types as rows.

For each configuration, we used a Monte Carlo procedure to estimate the expected Spearman correlation between f and d , and the expected p-value of the corresponding correlation test over the first n types, according to the sorting criterion for the ensemble of permutations of the original dataset. For every n between 5 and 58, expectations were estimated by averages over T randomizations of the dataset. Every randomization was produced permuting the contents of one of the columns of the matrix (f or d). We used $T = 10^5$.

In the absence of any statistical bias, the expected Spearman correlation should be zero [2] and the expected p-value should be 0.5. The latter follows from the fact that p-values are uniformly distributed within the interval $[0, 1]$ under the null hypothesis [3]. The expectation of a continuous random variable within the interval $[a, b]$ is $(a+b)/2$ [4]. In our case, the interval is $[0, 1]$ and then expected p-value is 0.5.

Results

Figure S3-1 shows the estimates of the expected Spearman correlation and the corresponding p-value as a function of n . When sorting by f and d , the estimates matched the theoretical predictions above. In contrast, sorting by D deviated from these predictions in two directions: for sufficiently low n , the Spearman correlation was negative and the p-value was below 0.5, indicating that sorting by D favours the emergence of the law of abbreviation. The curves produced in ascending order and those produced in descending order were very similar. In light of the findings above in relation to sorting by D , two questions arise: first, could the bias be attributed to the empirical distribution of values of f and d ? Notice that the permutations preserve the original values. The second and key question is: could sorting by D explain completely the emergence of the law of abbreviation in our dataset?

To address the first question, we controlled for role of the empirical distributions of values by replacing the true values of f and d by uniformly random numbers in the interval $[0,1]$. Qualitatively, the results were the same as those of the original data: a statistical bias when sorting by D and no statistical bias when sorting by f or d . Thus, the bias is not unique to our dataset.

To address the second question, we defined a new statistic: S , the average of the Spearman correlation between f and d over increasing length prefixes of the matrix up to length n after sorting rows by a certain variable in a certain order (ascending or descending). A prefix of the matrix of length i consists of the i first rows of the matrix (we have referred to prefixes as subsets, a more popular but ambiguous term, in the main article).

The statistic is defined as

$$S = \sum_{i=5}^n \rho_i,$$

where ρ_i is the Spearman correlation between f and d over the i top cells of the matrix after sorting the rows of the matrix in some way.

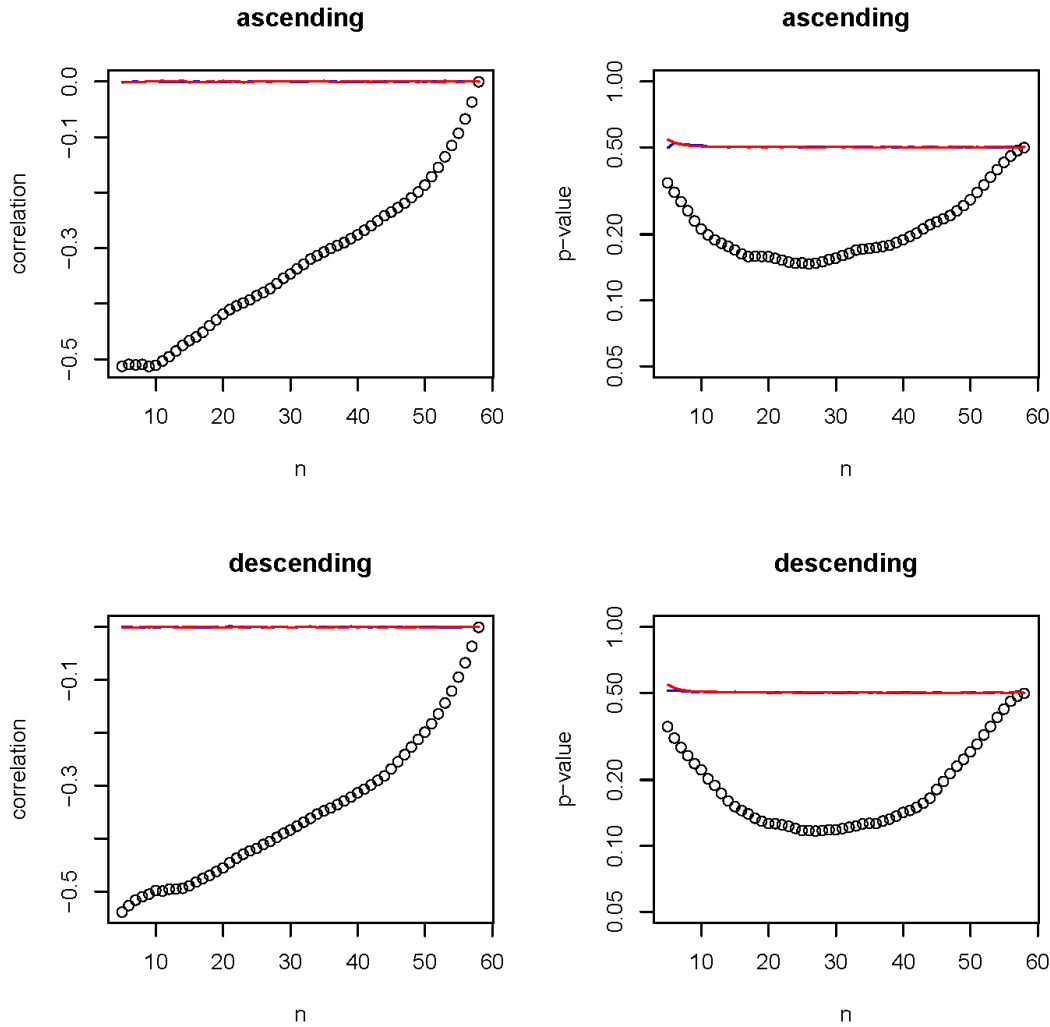


Figure S3-1: Estimates of the expected Spearman correlation and the expected p-value as a function of n when sorting by D (circles), f (blue line) and d (red line). Top: ascending order. Bottom: descending order.

For each of the six possible configurations, we took all values of n between 5 and 58 and calculated the true S and the corresponding p-value. The p-value was calculated using a Monte Carlo two-sided test to assess if the absolute value of S is significantly high with respect to the values of S that are obtained in randomizations of the original matrix that have been sorted according to the same criterion used to calculate the true S . The p-value was estimated over T^* randomizations of the matrix. We used $T^*=10^4$.

Figure 2 shows the value of the statistic S and the p-value of the Monte Carlos test of significance as a function of n . When sorting in ascending order by D , S was negative and tending to increase as n increases while the corresponding p-value was below the significance level from $n=7$ until about $n=40$. Therefore, sorting increasingly by D one finds a concordance with the law of abbreviation that cannot be fully explained by the prior bias seen in Figure S3-1, in accordance with our compression hypothesis. By contrast, when sorting in ascending order

by f and d , S was close to zero and the p-value was never below the significance level. Thus the law of abbreviation is missing in these orders.

When sorting in descending order by D , S was negative (as expected for the law of abbreviation) but the p-values were above 0.5 (Figure S3-2). Thus, selecting the gestures with the highest D , one obtains a concordance with the law of abbreviation that is an artifact of the bias reported in Figure S3-1.

When sorting in descending order by d , S was negative (as expected by the law of abbreviation) and small for sufficiently small n while the p-values passed below the significance level before $n = 20$. Thus, selecting the longest types one finds a concordance with the law of abbreviation that cannot be explained by any prior bias (recall Figure S3-1). This finding is consistent with the significant negative correlation between f and d for prefixes of length 6, 7, 12 and 13 reported in the main article. Our new supporting evidence could be due to the fact that S gives more weight to initial trends. To calculate S for a given prefix length n , the 5-th point participates in all the ρ_i 's, the 6-th point in all the ρ_i 's except one, the 7-th point in all the ρ_i 's except two,...and so on.

When sorting in descending order by f , S was positive (the opposite trend of the law of abbreviation) and never significant but the p-values reached a minimum close to the significance level for small n . Thus, selecting the most frequent types, a slight (though not significant) tendency to an anti-law of abbreviation was found for small n , a behavior that cannot be explained by any prior bias according to Figure S3-1.

To sum up, we reported in the main article that the law of abbreviation emerges when sorting gesture types by D and only rarely when sorting by f or d (ascending or descending). Our further analyses here support that for the ascending sorting by D and for a narrower domain in descending order by d , concordance with the law of abbreviation is not an artefact of sorting only.

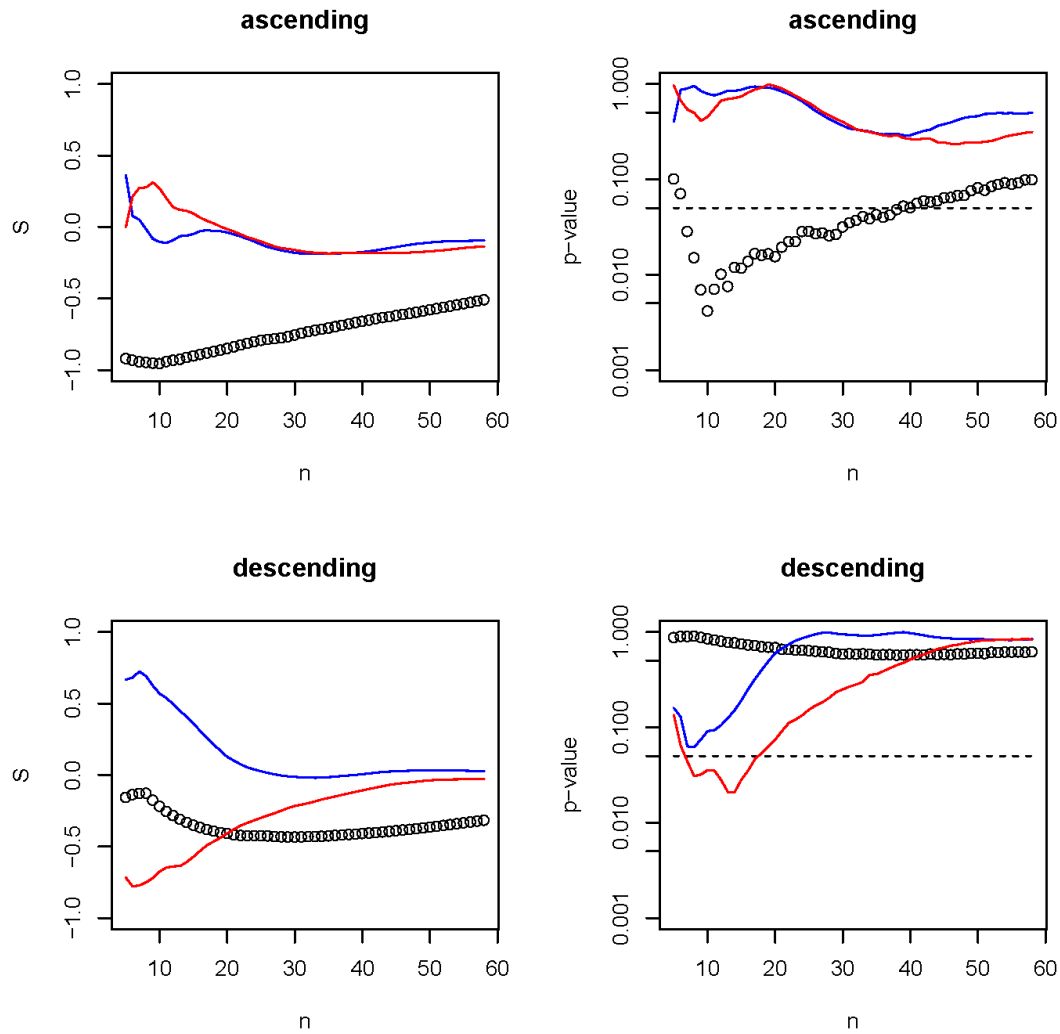


Figure S3-2: S , the average Spearman correlation statistic and the p-value of the Monte Carlo significance test as a function of n when sorting by D (circles), f (blue line) and d (red line). In the right subfigures, the dashed line indicates the significance level of 0.05. Top: ascending order. Bottom: descending order.

For completeness, Fig. S3-3 shows a comparison of the true values of S against the values of S that are obtained in the randomizations.

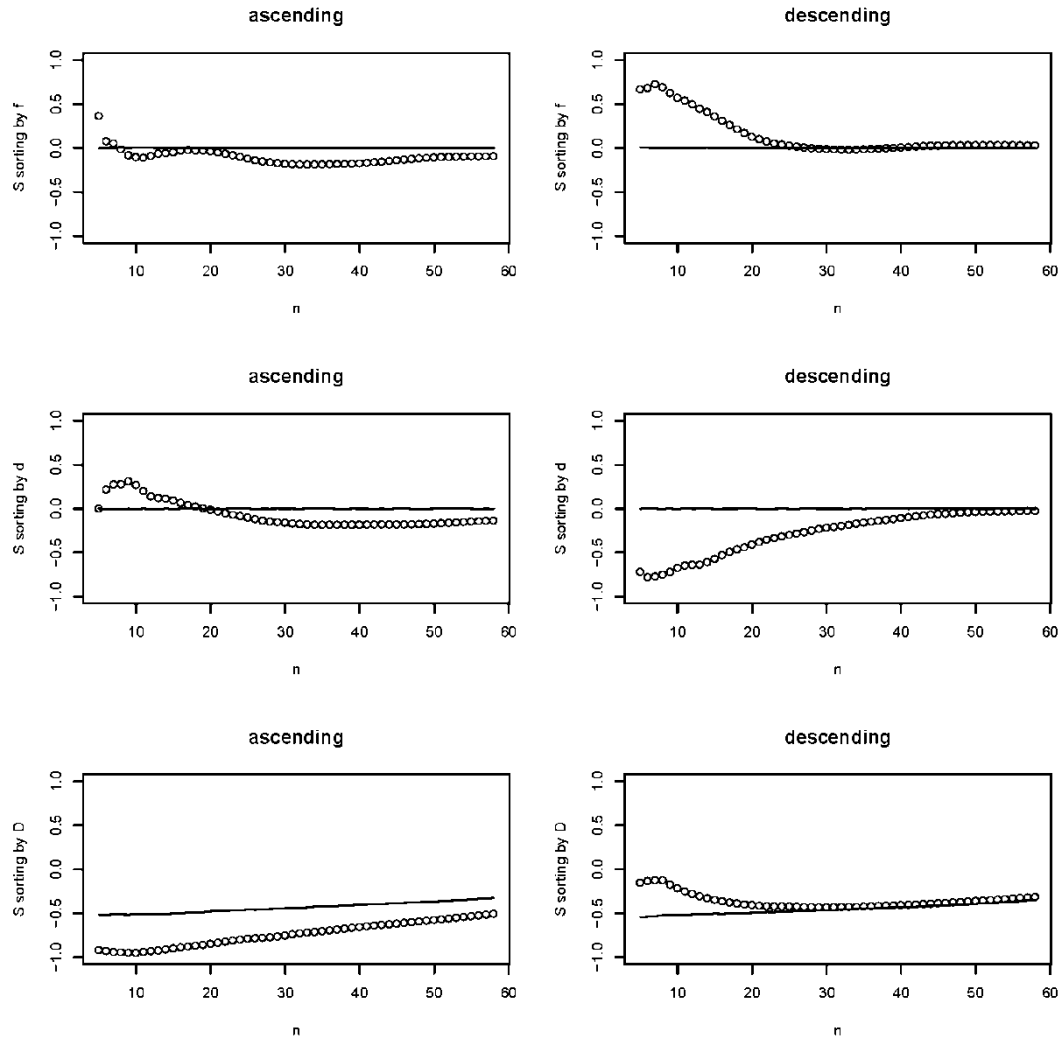


Figure S3-3. S , the true average Spearman correlation statistic (circles), against the same average in randomizations (solid line) for all six possible configurations. Left: ascending order. Right: descending order. Top: sorting by f . Centre: sorting by d . Bottom: sorting by D .

The following R code was used to generate the information needed for Figure S3-1.

```

replicas = 100000
random_data <- FALSE

run <- function(criterion, sign, file) {
  t <- read.table("DataL_processed.txt", header = TRUE)
  n <- nrow(t)
  if (!random_data) {
    f <- t$frequency
    d <- t$mean_duration
    D <- f*d
    t <- data.frame(f, d, D)
  }
  cat("Generating", file, "\r\n")
  sink(file)
  cat("length correlation_mean correlation_sd p_value_mean p_value_sd NA_counter\n")
  for (prefix_length in 5:n) {
    correlation_test <- data.frame(estimate = double(), p.value = double())
    NA_counter <- 0
    i <- 1
    while (i <= replicas) {
      if (random_data) {
        f <- runif(n, 0, 1)
        d <- runif(n, 0, 1)
        D <- f*d
        t <- data.frame(f, d, D)
      } else {
        d <- sample(t$d)
        t <- data.frame(f=t$f, d, D=t$f*d)
      }
      # Ordering criterion
      if (criterion == "D") {
        t <- t[order(sign*t$D),]
      } else if (criterion == "f") {
        t <- t[order(sign*t$f),]
      } else if (criterion == "d") {
        t <- t[order(sign*t$d),]
      }
      t_prefix <- t[1:prefix_length, ]
      correlation <- cor.test(t_prefix$f, t_prefix$d, method="spearman")
      if (is.na(correlation$estimate)) {
        NA_counter <- NA_counter + 1
      }
      else {
        new_row <- data.frame(estimate = correlation$estimate, p.value = correlation$p.value)
        correlation_test <- rbind(correlation_test, new_row)
        i <- i + 1
      }
    }
  }
}

```

```
stopifnot(nrow(correlation_test) == replicas)
average <- mean(correlation_test$estimate)
stopifnot(!is.na(average))
cat(prefix_length, average, sd(correlation_test$estimate), mean(correlation_test$p.value),
sd(correlation_test$p.value), NA_counter, "\n")
}
sink()
}

run("D", 1, "correlation_test_total_d_ascending.txt")
run("f", 1, "correlation_test_f_ascending.txt")
run("d", 1, "correlation_test_mean_d_ascending.txt")

run("D", -1, "correlation_test_total_d_descending.txt")
run("f", -1, "correlation_test_f_descending.txt")
run("d", -1, "correlation_test_mean_d_descending.txt")
```

The following R code was used to generate the information needed for Figures S3-2 and S3-3.

```
n_min <- 5
replicas = 10000

two_sided <- TRUE
input <- "DataL_processed.txt"

get_mean_correlation <- function(t, n, criterion, sign) {
  # Ordering criterion
  if (criterion == "D") {
    t <- t[order(sign*t$D),]
  } else if (criterion == "f") {
    t <- t[order(sign*t$f),]
  } else if (criterion == "d") {
    t <- t[order(sign*t$d),]
  }
  mean_correlation <- 0
  for(prefix_length in n_min:n) {
    t_prefix <- t[1:prefix_length, ]
    correlation <- cor.test(t_prefix$f, t_prefix$d, method="spearman")
    mean_correlation <- mean_correlation + correlation$estimate
  }
  mean_correlation <- mean_correlation/(n - n_min + 1)
  return (mean_correlation)
}

run <- function(criterion, sign, file) {
  t_original <- read.table(input, header = TRUE)
  n <- nrow(t_original)

  cat("Generating", file,"\r\n")
  sink(file)
  cat("length correlation correlation_random p_value NA_counter\r\n")
  for (prefix_length in n_min:n) {
    t <- t_original
    f <- t$frequency
    d <- t$mean_duration
    D <- f*d
    t <- data.frame(f, d, D)
    NA_counter <- 0
    mean_true <- get_mean_correlation(t, prefix_length, criterion, sign) # this is the statistic of
the test
    correlation_random <- 0
    m <- 0
    for (i in 1:replicas) {
      repeat {
        d <- sample(t$d)
```

```

t <- data.frame(f=t$f, d, D=t$f*d)
mean_random <- get_mean_correlation(t, prefix_length, criterion, sign)
  if (is.na(mean_random)) {
    NA_counter <- NA_counter + 1
  } else {
    break
  }
}
if (two_sided) {
  increment <- abs(mean_random) > abs(mean_true)
} else {
  # one sided test
  increment <- mean_random < mean_true
}
if (increment) {
  m <- m + 1
}
p_value <- m/i
correlation_random <- correlation_random + mean_random
}
correlation_random <- correlation_random/replicas
cat(prefix_length, mean_true, correlation_random, p_value, NA_counter, "\r\n")
}
sink()
}

run("D", 1, "sorting_effect_test_total_d_ascending.txt")
run("f", 1, "sorting_effect_test_f_ascending.txt")
run("d", 1, "sorting_effect_test_mean_d_ascending.txt")

run("D", -1, "sorting_effect_test_total_d_descending.txt")
run("f", -1, "sorting_effect_test_f_descending.txt")
run("d", -1, "sorting_effect_test_mean_d_descending.txt")

```

S4

Mean duration and frequency of use (for each age class) of play gesture types. *S.D.* denotes standard deviation

Gesture Type	Mean	S.D.	Frequency	Nature	Infant	Juvenile	Subadult	Adult
Arm raise	1.07	0.34	11	Manual Gesture	1	7	3	0
Arm shake	3.29	2.29	18	Manual Gesture	1	10	7	0
Arm swing	2.03	1.34	137	Manual Gesture	20	85	32	0
Arm wave	1.61	0.92	3	Manual Gesture	0	2	1	0
Bite	3.46	2.47	66	Manual Gesture	14	31	18	3
Bow	2.06	1.10	2	Whole Body Signal	0	1	1	0
Clap	0.94	0.14	2	Manual Gesture	2	0	0	0
Dangle	6.14	5.59	229	Whole Body Signal	90	114	25	0
Directed push	12.72	0.00	1	Manual Gesture	0	0	1	0
Drum object	1.22	0.67	6	Manual Gesture	1	4	1	0
Drum other	1.53	0.81	4	Manual Gesture	1	3	0	0
Embrace	2.97	0.56	5	Manual Gesture	2	2	0	1
Feet shake	2.79	2.66	16	Manual Gesture	2	5	9	0
Gallop	3.81	2.02	23	Whole Body Signal	2	16	5	0
Grab	3.58	3.84	229	Manual Gesture	48	88	78	15
Grab-pull	3.59	2.37	44	Manual Gesture	4	13	24	3
Hand on	7.58	6.36	46	Manual Gesture	4	9	21	12
Hand shake	1.09	0.30	9	Manual Gesture	0	3	6	0
Head butt	1.60	0.00	1	Whole Body Signal	0	0	1	0
Head nod	3.02	3.75	17	Manual Gesture	0	4	11	2
Head stand	5.57	5.31	29	Whole Body Signal	1	14	13	1
Hide face	3.44	0.85	2	Manual Gesture	0	0	2	0
Hit with object	1.32	0.96	2	Manual Gesture	1	0	1	0
Jump	0.54	0.16	7	Whole Body Signal	3	2	2	0
Kick	0.87	0.57	73	Manual Gesture	7	11	55	0
Knock object	0.72	0.28	4	Manual Gesture	1	1	2	0
Leaf clipping	11.51	7.29	3	Manual Gesture	0	2	1	0
Leg swing	2.24	1.60	14	Manual Gesture	1	11	2	0
Look	1.60	0.00	1	Whole Body Signal	0	0	1	0
Object in mouth	6.95	4.70	27	Manual Gesture	11	14	2	0
Object move	2.00	1.50	97	Manual Gesture	25	37	34	1
Object shake	2.94	2.02	80	Manual Gesture	10	37	33	0
Pirouette	3.40	3.64	3	Whole Body Signal	1	2	0	0
Poke	1.21	0.65	10	Manual Gesture	0	3	5	2
Pounce	0.88	0.28	5	Whole Body Signal	0	3	2	0
Punch object/ground	0.58	0.34	25	Manual Gesture	12	10	2	1
Punch other	0.81	0.30	6	Manual Gesture	0	3	2	1
Push	2.18	3.14	10	Manual Gesture	2	4	4	0
Reach	3.24	2.68	66	Manual Gesture	18	21	22	5
Roll over	4.48	3.23	29	Whole Body Signal	1	16	11	1
Side roulade	3.08	1.92	9	Whole Body Signal	2	7	0	0
Slap object	0.69	0.53	128	Manual Gesture	14	74	40	0
Slap object with object	0.76	0.25	3	Manual Gesture	0	3	0	0
Slap other	0.86	2.86	158	Manual Gesture	82	66	9	1
Somersault	3.88	2.90	28	Whole Body Signal	10	11	7	0
Stiff walk	3.31	1.85	3	Whole Body Signal	0	1	2	0
Stomp	0.59	0.25	155	Manual Gesture	36	91	28	0
Stomp 2-feet	0.60	0.25	73	Manual Gesture	27	32	14	0
Stomp 2-feet alternate	2.07	0.93	23	Manual Gesture	7	12	4	0
Stomp 2-feet other	0.64	0.29	19	Manual Gesture	13	6	0	0
Stomp 2-feet other alternate	1.10	0.20	2	Manual Gesture	0	2	0	0
Stomp other	0.58	0.17	8	Manual Gesture	4	4	0	0
Tandem walk	2.04	0.00	1	Whole Body Signal	0	1	0	0
Tap object	0.43	0.13	5	Manual Gesture	0	5	0	0
Tap other	0.40	0.31	101	Manual Gesture	1	16	77	7
Throw object	3.06	3.14	2	Manual Gesture	0	2	0	0
Touch other	1.53	0.56	54	Manual Gesture	10	16	17	11
Water splash	17.19	7.21	3	Manual Gesture	0	3	0	0
58	2.85	1.87	2137	-	492	940	638	67

S5A**R Code for the calculation and significance testing of L**

```
data1 <- read.table ("DataL_processed.txt", header=T)

reps <- 100000

results <- rep(0, reps)

x <- c(data1$probability)
y <- c(data1$mean_duration)

L <- sum(x*y)

print (c("real L is", L))

sortvector <- 1:length(x)
for (i in 1:reps)
{
  sortvector <- sample(sortvector, replace = F)
  xtemp <- x[sortvector]
  L_temp <- sum(xtemp *y)
  results[i] <- L_temp
}
hist(results)

is_small <- sum(results < L)

print(c("P of being so small is estimated as ", is_small/reps))
```

S5B**R Code for the calculation and significance testing of M**

```
data1 <- read.table("DataM_sequence_1gesture.txt ", header=T)
reps <- 100000

results <- rep(0, reps)

x <- c(data1$Sequence_Size)
y <- c(data1$mean_duration)

M <- sum(x*y)

print(c("real M is", M))

sortvector <- 1:length(x)
for (i in 1:reps)
{
  sortvector <- sample(sortvector, replace = F)
  xtemp <- x[sortvector]
  M_temp <- sum(xtemp *y)
  results[i] <- M_temp
}
hist(results)

is_small <- sum(results < M)

print(c("P of being so small is estimated as ", is_small/reps))
```

Results of analyses of subsets of play gestures, ordered from low to high values of D , and from high to low values of D . Significant results are highlighted in grey. Values for L are indicated in seconds.

Order of gesture types				Spearman's correlation test for D				Spearman correlation tests for control analysis for D				L for D			
Gesture type (low to high D)	i (low to high D)	Gesture type (high to low D)	i (high to low D)	r_s (low to high D)	p	r_s (high to low D)	p	r_s (low to high D)	p	r_s (high to low D)	p	L (low to high D)	p	L (high to low D)	p
	0	Look	58	na	na	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42
Look	1	Head butt	57	na	na	-0.01	0.93	na	na	0.85	<0.001	na	na	2.65	0.4
Head butt	2	Clap	56	na	na	-0.02	0.88	na	na	0.84	<0.001	na	na	2.65	0.39
Clap	3	Tandem walk	55	na	na	-0.04	0.79	na	na	0.84	<0.001	na	na	2.65	0.36
Tandem walk	4	Tap object	54	na	na	-0.04	0.78	na	0.73	0.83	<0.001	na	na	2.65	0.35
Tap object	5	Stomp 2-feet other alternate	53	-0.92	0.03	-0.06	0.68	0.69	0.2	0.84	<0.001	0.93	<0.001	2.65	0.32
Stomp 2-feet other alternate	6	Slap object with object	52	-0.94	0.01	-0.08	0.6	0.69	0.13	0.83	<0.001	0.96	<0.001	2.66	0.3
Slap object with object	7	Hit with object	51	-0.96	<0.001	-0.1	0.5	0.74	0.06	0.83	<0.001	0.92	<0.001	2.66	0.27
Hit with object	8	Knock object	50	-0.96	<0.001	-0.11	0.43	0.66	0.08	0.82	<0.001	0.96	<0.001	2.66	0.25
Knock object	9	Jump	49	-0.97	<0.001	-0.13	0.37	0.69	0.04	0.82	<0.001	0.92	<0.001	2.66	0.22
Jump	10	Bow	48	-0.97	<0.001	-0.16	0.28	0.78	0.01	0.82	<0.001	0.82	<0.001	2.67	0.19
Bow	11	Pounce	47	-0.86	<0.01	-0.17	0.26	0.65	0.03	0.82	<0.001	0.91	<0.001	2.67	0.18
Pounce	12	Stomp other	46	-0.86	<0.001	-0.18	0.23	0.69	0.01	0.82	<0.001	0.9	<0.001	2.67	0.15
Stomp other	13	Punch other	45	-0.87	<0.001	-0.22	0.16	0.76	<0.01	0.82	<0.001	0.84	<0.001	2.68	0.13
Punch other	14	Arm wave	44	-0.85	<0.001	-0.24	0.12	0.79	<0.01	0.82	<0.001	0.84	<0.001	2.68	0.11

Order of gesture types				Spearman's correlation test for D				Spearman correlation tests for control analysis for D				L for D			
Gesture type (low to high D)	i (low to high D)	Gesture type (high to low D)	i (high to low D)	r_s (low to high D)	p	r_s (high to low D)	p	r_s (low to high D)	p	r_s (high to low D)	p	L (low to high D)	p	L (high to low D)	p
Arm wave	15	Throw object	43	-0.79	<0.001	-0.26	0.09	0.73	<0.01	0.81	<0.001	0.88	<0.001	2.68	0.09
Throw object	16	Drum other	42	-0.77	<0.001	-0.26	0.1	0.6	0.02	0.8	<0.001	0.96	<0.001	2.69	0.09
Drum other	17	Hide face	41	-0.76	<0.001	-0.28	0.08	0.57	0.02	0.79	<0.001	1	<0.001	2.69	0.07
Hide face	18	Drum object (palms)	40	-0.74	<0.001	-0.27	0.09	0.47	0.05	0.78	<0.001	1.1	<0.001	2.69	0.08
Drum object (palms)	19	Hand shake	39	-0.71	<0.01	-0.3	0.07	0.52	0.02	0.77	<0.001	1.1	<0.001	2.69	0.06
Hand shake	20	Stiff walk	38	-0.68	<0.01	-0.32	0.05	0.59	0.01	0.77	<0.001	1.1	<0.01	2.7	0.05
Stiff walk	21	Pirouette	37	-0.64	<0.01	-0.32	0.06	0.54	0.01	0.75	<0.001	1.18	<0.01	2.7	0.05
Pirouette	22	Arm raise	36	-0.61	<0.01	-0.31	0.06	0.5	0.02	0.73	0.003	1.26	<0.01	2.7	0.05
Arm raise	23	Poke	35	-0.6	<0.01	-0.34	0.04	0.56	0.01	0.72	0.009	1.24	<0.01	2.71	0.03
Poke	24	Stomp 2-feet other	34	-0.57	<0.01	-0.38	0.03	0.62	<0.01	0.71	<0.001	1.24	<0.01	2.72	0.02
Stomp 2-feet other	25	Directed push	33	-0.61	<0.01	-0.42	0.02	0.66	<0.001	0.71	<0.001	1.14	<0.01	2.74	0.02
Directed push	26	Punch object/ground	32	-0.65	<0.001	-0.36	0.04	0.45	0.01	0.68	<0.001	1.24	<0.001	2.73	0.04
Punch object/ground	27	Embrace	31	-0.67	<0.001	-0.41	0.02	0.55	<0.01	0.68	<0.001	1.13	<0.001	2.76	0.03
Embrace	28	Push	30	-0.64	<0.001	-0.43	0.02	0.55	<0.01	0.65	<0.001	1.19	<0.001	2.76	0.02
Push	29	Side roulade	29	-0.56	<0.01	-0.46	0.01	0.59	<0.01	0.62	<0.001	1.25	<0.001	2.76	0.02
Side roulade	30	Leg swing	28	-0.48	<0.01	-0.48	0.01	0.61	<0.001	0.58	<0.01	1.34	<0.01	2.76	0.01
Leg swing	31	Leaf clipping	27	-0.41	0.02	-0.52	<0.01	0.65	<0.001	0.54	<0.01	1.41	<0.001	2.76	0.01
Leaf clipping	32	Tap other	26	-0.42	0.02	-0.46	0.02	0.59	<0.001	0.49	0.01	1.57	0.01	2.75	0.03

Order of gesture types				Spearman's correlation test for D				Spearman correlation tests for control analysis for D				L for D			
Gesture type (low to high D)	i (low to high D)	Gesture type (high to low D)	i (high to low D)	r_s (low to high D)	p	r_s (high to low D)	p	r_s (low to high D)	p	r_s (high to low D)	p	L (low to high D)	p	L (high to low D)	p
Tap other	33	Stomp 2-feet	25	-0.47	0.01	-0.43	0.03	0.63	<0.001	0.59	<0.01	1.16	<0.001	2.88	0.04
Stomp 2-feet	34	Feet shake	24	-0.5	<0.01	-0.41	0.05	0.66	<0.001	0.68	<0.001	1.05	<0.001	2.97	0.04
Feet shake	35	Stomp 2-feet alternate	23	-0.45	<0.01	-0.46	0.03	0.63	<0.001	0.63	<0.01	1.12	<0.001	2.97	0.03
Stomp 2-feet alternate	36	Head nod	22	-0.41	0.01	-0.51	0.02	0.7	<0.001	0.59	<0.01	1.18	<0.01	2.98	0.03
Head nod	37	Water splash. 1 hand	21	-0.36	0.03	-0.56	0.01	0.72	0.01	0.53	0.01	1.25	<0.01	2.98	0.02
Water splash, 1 hand	38	Arm shake	20	-0.37	0.02	-0.5	0.03	0.66	<0.001	0.46	0.04	1.37	<0.01	2.96	0.13
Arm shake	39	Kick	19	-0.33	0.04	-0.54	0.02	0.68	<0.001	0.37	0.12	1.45	<0.01	2.96	0.13
Kick	40	Touch other	18	-0.36	0.02	-0.53	0.02	0.7	0.01	0.42	0.08	1.36	<0.01	3.05	0.11
Touch other	41	Gallop	17	-0.35	0.02	-0.55	0.02	0.72	<0.01	0.44	0.08	1.38	<0.01	3.1	0.08
Gallop	42	Slap object	16	-0.3	0.06	-0.55	0.03	0.73	<0.001	0.32	0.22	1.47	<0.01	3.09	0.09
Slap object	43	Stomp	15	-0.34	0.03	-0.54	0.04	0.75	<0.001	0.44	0.1	1.33	<0.01	3.31	0.11
Stomp	44	Somersault	14	-0.37	0.01	-0.53	0.06	0.77	<0.001	0.64	0.01	1.2	<0.01	3.64	0.18
Somersault	45	Roll over	13	-0.32	0.03	-0.51	0.07	0.78	<0.001	0.58	0.04	1.29	<0.01	3.64	0.18
Roll over	46	Slap other	12	-0.27	0.07	-0.48	0.11	0.79	<0.001	0.51	0.09	1.38	<0.01	3.62	0.19
Slap other	47	Grab-pull	11	-0.3	0.04	-0.47	0.15	0.8	<0.001	0.77	0.01	1.31	<0.01	4.03	0.31
Grab-pull	48	Head stand	10	-0.26	0.08	-0.43	0.22	0.81	<0.001	0.73	0.02	1.4	<0.01	4.05	0.28
Head stand	49	Object in mouth	9	-0.22	0.13	-0.37	0.33	0.81	<0.001	0.64	0.06	1.5	<0.01	4	0.35
Object in mouth	50	Object move	8	-0.18	0.2	-0.12	0.78	0.82	<0.001	0.48	0.23	1.63	0.01	3.92	0.55
Object move	51	Reach	7	-0.18	0.21	-0.11	0.82	0.82	<0.001	0.62	0.14	1.65	0.02	4.14	0.5

Order of gesture types				Spearman's correlation test for D				Spearman correlation tests for control analysis for D				L for D			
Gesture type (low to high D)	i (low to high D)	Gesture type (high to low D)	i (high to low D)	r_s (low to high D)	p	r_s (high to low D)	p	r_s (low to high D)	p	r_s (high to low D)	p	L (low to high D)	p	L (high to low D)	p
Reach	52	Bite	6	-0.16	0.27	-0.12	0.83	0.83	<0.001	0.64	0.173	1.73	0.02	4.21	0.44
Bite	53	Object shake	5	-0.13	0.36	-0.15	0.81	0.83	<0.001	0.67	0.22	1.81	0.03	4.28	0.37
Object shake	54	Arm swing	4	-0.11	0.41	na	na	0.84	<0.001	na	na	1.87	0.04	na	na
Arm swing	55	Hand on	3	-0.11	0.43	na	na	0.84	<0.001	na	na	1.89	0.04	na	na
Hand on	56	Grab	2	-0.09	0.52	na	na	0.84	<0.001	na	na	2.04	0.07	na	na
Grab	57	Dangle	1	-0.05	0.73	na	na	0.85	<0.001	na	na	2.23	0.16	na	na
Dangle	58		0	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42	na	na

S7

Results of analyses of subsets of play gestures, ordered from low to high values of f , and from high to low values of f . Significant results are highlighted in grey. Values for L are indicated in seconds.

Order of gesture types				Spearman's correlation test for f				Spearman correlation tests for control analysis for f				L for f			
Gesture type (low to high f)	i (low to high f)	Gesture type (high to low f)	i (high to low f)	r_s (low to high f)	p	r_s (high to low f)	p	r_s (low to high f)	p	r_s (high to low f)	p	L (low to high f)	p	L (high to low f)	p
	0	Look	58	na	na	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42
Look	1	Head butt	57	na	na	0.04	0.742	na	na	0.85	<0.001	na	na	2.65	0.41
Head butt	2	Tandem walk	56	na	na	0.05	0.736	na	na	0.84	<0.001	na	na	2.65	0.39
Tandem walk	3	Directed push	55	na	na	0.04	0.772	na	na	0.84	<0.001	na	na	2.65	0.38
Directed push	4	Clap	54	na	na	0.03	0.81	na	na	0.85	<0.001	na	na	2.64	0.5
Clap	5	Stomp 2-feet other alternate	53	-0.73	0.17	0.06	0.691	na	na	0.84	<0.001	3.31	<0.001	2.64	0.47
Stomp 2-feet other alternate	6	Hit with object	52	-0.84	0.04	0.07	0.611	0.21	0.69	0.84	<0.001	2.76	<0.001	2.65	0.45
Hit with object	7	Bow	51	-0.87	0.01	0.07	0.602	0.29	0.53	0.83	<0.001	2.47	<0.001	2.65	0.43
Bow	8	Throw object	50	-0.55	0.16	0.06	0.657	0.33	0.43	0.82	<0.001	2.4	0.06	2.65	0.41
Throw object	9	Hide face	49	-0.35	0.36	0.05	0.734	0.35	0.36	0.82	<0.001	2.49	0.19	2.65	0.42
Hide face	10	Slap object with object	48	-0.21	0.55	0.03	0.84	0.36	0.31	0.82	<0.001	2.61	0.25	2.65	0.43
Slap object with object	11	Arm wave	47	-0.43	0.18	0.09	0.537	0.31	0.36	0.81	<0.001	2.32	0.11	2.65	0.4
Arm wave	12	Stiff walk	46	-0.34	0.27	0.16	0.288	0.33	0.30	0.81	<0.001	2.22	0.1	2.65	0.37
Stiff walk	13	Pirouette	45	-0.17	0.58	0.19	0.2	0.40	0.18	0.81	<0.001	2.35	0.17	2.65	0.39
Pirouette	14	Leaf clipping	44	-0.05	0.87	0.23	0.129	0.45	0.11	0.80	<0.001	2.47	0.22	2.65	0.4
Leaf clipping	15	Water splash. 1 hand	43	0.07	0.81	0.23	0.13	0.52	0.05	0.82	<0.001	3.34	0.48	2.64	0.54

Order of gesture types				Spearman's correlation test for f				Spearman correlation tests for control analysis for f				L for f			
Gesture type (low to high f)	i (low to high f)	Gesture type (high to low f)	i (high to low f)	r_s (low to high f)	p	r_s (high to low f)	p	r_s (low to high f)	p	r_s (high to low f)	p	L (low to high f)	p	L (high to low f)	p
Water splash, 1 hand	16	Knock object	42	0.19	0.49	0.21	0.18	0.58	0.02	0.85	<0.001	4.56	0.75	2.61	0.81
Knock object	17	Drum other	41	-0.21	0.94	0.21	0.187	0.50	0.04	0.84	<0.001	4.16	0.61	2.62	0.78
Drum other	18	Tap object	40	-0.11	0.67	0.18	0.25	0.47	0.05	0.83	<0.001	3.91	0.53	2.62	0.76
Tap object	19	Pounce	39	-0.25	0.31	0.21	0.2	0.35	0.14	0.82	<0.001	3.54	0.39	2.63	0.72
Pounce	20	Embrace	38	-0.35	0.14	0.2	0.237	0.32	0.17	0.81	<0.001	3.28	0.3	2.63	0.69
Embrace	21	Punch other	37	-0.27	0.23	0.14	0.42	0.38	0.09	0.81	<0.001	3.26	0.3	2.63	0.7
Punch other	22	Drum object (palms)	36	-0.35	0.11	0.12	0.476	0.36	0.10	0.79	<0.001	3.02	0.22	2.63	0.66
Drum object (palms)	23	Jump	35	-0.38	0.07	0.09	0.62	0.38	0.08	0.77	<0.001	2.87	0.18	2.64	0.62
Jump	24	Stomp other	34	-0.46	0.03	0.01	0.95	0.33	0.12	0.75	<0.001	2.65	0.13	2.65	0.56
Stomp other	25	Hand shake	33	-0.52	0.01	-0.07	0.7	0.30	0.14	0.73	<0.001	2.45	0.08	2.65	0.5
Hand shake	26	Side roulade	32	-0.53	0.01	-0.06	0.741	0.33	0.10	0.7	<0.001	2.32	0.06	2.66	0.45
Side roulade	27	Poke	31	-0.43	0.03	-0.1	0.6	0.38	0.05	0.68	<0.001	2.39	0.09	2.66	0.46
Poke	28	Push	30	-0.43	0.02	-0.11	0.581	0.41	0.03	0.65	<0.001	2.28	0.07	2.67	0.41
Push	29	Arm raise	29	-0.36	0.05	-0.15	0.45	0.45	0.01	0.62	<0.001	2.28	0.08	2.67	0.39
Arm raise	30	Leg swing	28	-0.39	0.04	-0.20	0.32	0.47	0.01	0.58	<0.01	2.18	0.06	2.67	0.32
Leg swing	31	Feet shake	27	-0.32	0.08	-0.21	0.29	0.51	0.00	0.54	<0.01	2.18	0.07	2.68	0.3
Feet shake	32	Head nod	26	-0.26	0.15	-0.23	0.27	0.55	0.00	0.52	0.01	2.24	0.1	2.68	0.3
Head nod	33	Arm shake	25	-0.21	0.25	-0.23	0.27	0.58	<0.001	0.49	0.01	2.31	0.15	2.68	0.31
Arm shake	34	Stomp 2-feet other	24	-0.14	0.42	-0.22	0.29	0.62	<0.001	0.46	0.03	2.4	0.2	2.67	0.32
Stomp 2-feet other	35	Stomp 2-feet alternate	23	-0.21	0.24	-0.34	0.12	0.62	<0.001	0.38	0.07	2.25	0.14	2.69	0.24
Stomp 2-feet alternate	36	Gallop	22	-0.17	0.33	-0.3	0.175	0.64	<0.001	0.33	0.13	2.23	0.14	2.7	0.21

Order of gesture types				Spearman's correlation test for f				Spearman correlation tests for control analysis for f				L for f			
Gesture type (low to high f)	i (low to high f)	Gesture type (high to low f)	i (high to low f)	r_s (low to high f)	p	r_s (high to low f)	p	r_s (low to high f)	p	r_s (high to low f)	p	L (low to high f)	p	L (high to low f)	p
Gallop	37	Punch object/ground	21	-0.1	0.58	-0.33	0.15	0.67	<0.001	0.29	0.2	2.37	0.22	2.68	0.24
Punch object/ground	38	Object in mouth	20	-0.16	0.35	-0.51	0.02	0.67	<0.001	0.18	0.45	2.21	0.15	2.71	0.15
Object in mouth	39	Somersault	19	-0.09	0.60	-0.44	0.06	0.69	<0.001	0.21	0.39	2.62	0.37	2.65	0.27
Somersault	40	Roll over	18	-0.02	0.88	-0.39	0.11	0.72	<0.001	0.20	0.43	2.72	0.42	2.63	0.32
Roll over	41	Head stand	17	0.03	0.84	-0.33	0.20	0.74	<0.001	0.19	0.47	2.86	0.5	2.6	0.41
Head stand	42	Grab-pull	16	0.08	0.60	-0.25	0.36	0.75	<0.001	0.22	0.42	3.06	0.59	2.55	0.58
Grab-pull	43	Hand on	15	0.13	0.41	-0.14	0.62	0.77	<0.001	0.25	0.36	3.11	0.62	2.52	0.64
Hand on	44	Touch other	14	0.17	0.26	0.06	0.83	0.79	<0.001	0.42	0.13	3.53	0.8	2.38	0.92
Touch other	45	Reach	13	0.15	0.33	0.06	0.84	0.80	<0.001	0.36	0.23	3.33	0.71	2.41	0.91
Reach	46	Bite	12	0.17	0.26	0.19	0.56	0.81	<0.001	0.48	0.12	3.32	0.7	2.32	0.94
Bite	47	Stomp 2-feet	11	0.2	0.17	0.36	0.28	0.82	<0.001	0.64	0.03	3.33	0.71	2.33	0.97
Stomp 2-feet	48	Kick	10	0.14	0.35	0.43	0.22	0.82	<0.001	0.57	0.08	3.07	0.58	2.42	0.96
Kick	49	Object shake	9	0.09	0.54	0.36	0.34	0.82	<0.001	0.46	0.21	2.87	0.48	2.5	0.94
Object shake	50	Object move	8	0.1	0.48	0.59	0.13	0.83	<0.001	0.64	0.09	2.88	0.48	2.47	0.97
Object move	51	Tap other	7	0.1	0.50	0.81	0.03	0.84	<0.001	0.88	0.01	2.79	0.43	2.52	0.98
Tap other	52	Slap object	6	0.04	0.81	0.70	0.13	0.83	<0.001	0.81	0.05	2.57	0.3	2.72	0.96
Slap object	53	Arm swing	5	-0.01	0.93	0.67	0.22	0.83	<0.001	0.67	0.22	2.38	0.2	2.67	0.95
Arm swing	54	Stomp	4	-0.01	0.94	na	na	0.84	<0.001	na	na	2.34	0.19	na	na

Order of gesture types				Spearman's correlation test for f				Spearman correlation tests for control analysis for f				L for f			
Gesture type (low to high f)	i (low to high f)	Gesture type (high to low f)	i (high to low f)	r_s (low to high f)	p	r_s (high to low f)	p	r_s (low to high f)	p	r_s (high to low f)	p	L (low to high f)	p	L (high to low f)	p
Stomp	55	Slap other	3	-0.06	0.69	na	na	0.84	<0.001	na	na	2.164	0.11	na	na
Slap other	56	Grab	2	-0.09	0.52	na	na	0.84	<0.001	na	na	2.04	0.07	na	na
Grab	57	Dangle	1	-0.05	0.73	na	na	0.85	<0.001	na	na	2.23	0.16	na	na
Dangle	58		0	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42	na	na

6

S8

7

Results of analyses of subsets of play gestures, ordered from low to high values of d , and from high to low values of d . Significant results are highlighted in grey. Values for L are indicated in seconds.

8

Order of gesture types				Spearman's correlation test for d				Spearman correlation tests for control analysis for d				L for d			
Gesture type (low to high d)	i (low to high d)	Gesture type (high to low d)	i (high to low d)	r_s (low to high d)	p	r_s high to low d	p	r_s (low to high d)	p	r_s (high to low d)	p	L (low to high d)	p	L (high to low d)	p
	0	Tap other	58	na	na	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42
Tap other	1	Tap object	57	na	na	0.04	0.78	na	na	0.87	<0.001	na	na	2.76	0.48
Tap object	2	Jump	56	na	na	0.03	0.85	na	na	0.87	<0.001	na	na	2.76	0.45
Jump	3	Stomp other	55	na	na	0.01	0.92	na	na	0.88	<0.001	na	na	2.77	0.42
Stomp other	4	Punch object/ground	54	na	na	0.00	0.98	na	na	0.88	<0.001	na	na	2.77	0.42
Punch object/ground	5	Stomp	53	-0.05	0.94	0.02	0.91	1	0.02	0.88	<0.001	0.45	0.23	2.78	0.4
Stomp	6	Stomp 2-feet	52	0.41	0.43	0.07	0.64	1	<0.001	0.89	<0.001	0.52	0.52	2.81	0.39
Stomp 2-feet	7	Stomp 2-feet other	51	0.38	0.40	0.12	0.42	0.96	<0.001	0.90	<0.001	0.54	0.54	3.1	0.53
Stomp 2-feet other	8	Slap object	50	0.26	0.53	0.13	0.37	0.98	<0.001	0.90	<0.001	0.54	0.44	3.12	0.52
Slap object	9	Knock object	49	0.44	0.24	0.19	0.20	0.98	<0.001	0.90	<0.001	0.58	0.69	3.31	0.6
Knock object	10	Slap object with object	48	0.04	0.91	0.18	0.22	0.98	<0.001	0.91	<0.001	0.58	0.69	3.32	0.57
Slap object with object	11	Punch other	47	-0.22	0.52	0.16	0.29	0.96	<0.001	0.91	<0.001	0.58	0.69	3.32	0.55
Punch other	12	Slap other	46	-0.31	0.33	0.15	0.31	0.95	<0.001	0.92	<0.001	0.58	0.69	3.33	0.52
Slap other	13	Kick	45	-0.03	0.93	0.22	0.14	0.96	<0.001	0.92	<0.001	0.65	0.64	3.6	0.64
Kick	14	Pounce	44	0.04	0.88	0.29	0.06	0.96	<0.001	0.92	<0.001	0.67	0.68	3.75	0.68
Pounce	15	Clap	43	-0.10	0.73	0.29	0.06	0.95	<0.001	0.93	<0.001	0.67	0.55	3.76	0.66

Order of gesture types				Spearman's correlation test for d				Spearman correlation tests for control analysis for d				L for d			
Gesture type (low to high d)	i (low to high d)	Gesture type (high to low d)	i (high to low d)	r_s (low to high d)	p	r_s high to low d	p	r_s (low to high d)	p	r_s (high to low d)	p	L (low to high d)	p	L (high to low d)	p
Clap	16	Arm raise	42	-0.26	0.34	0.26	0.10	0.96	<0.001	0.93	<0.001	0.67	0.41	3.76	0.63
Arm raise	17	Hand shake	41	-0.23	0.38	0.26	0.10	0.97	<0.001	0.93	<0.001	0.68	0.31	3.78	0.61
Hand shake	18	Stomp 2-feet other alternate	40	-0.20	0.42	0.26	0.10	0.97	<0.001	0.94	<0.001	0.68	0.23	3.8	0.59
Stomp 2-feet other alternate	19	Poke	39	-0.32	0.18	0.22	0.17	0.97	<0.001	0.93	<0.001	0.68	0.16	3.81	0.56
Poke	20	Drum object (palms)	38	-0.28	0.23	0.22	0.18	0.97	<0.001	0.94	<0.001	0.69	0.12	3.83	0.54
Drum object (palms)	21	Hit with object	37	-0.31	0.18	0.22	0.20	0.97	<0.001	0.94	<0.001	0.69	0.09	3.84	0.5
Hit with object	22	Drum other	36	-0.39	0.07	0.17	0.32	0.96	<0.001	0.94	<0.001	0.69	0.06	3.84	0.46
Drum other	23	Touch other	35	-0.44	0.04	0.16	0.37	0.95	<0.001	0.95	<0.001	0.7	0.04	3.85	0.45
Touch other	24	Look	34	-0.35	0.09	0.23	0.20	0.95	<0.001	0.95	<0.001	0.75	0.08	3.95	0.45
Look	25	Head butt	33	-0.43	0.03	0.16	0.37	0.95	<0.001	0.95	<0.001	0.75	0.06	3.95	0.41
Head butt	26	Arm wave	32	-0.49	0.01	0.09	0.64	0.96	<0.001	0.95	<0.001	0.75	0.06	3.95	0.36
Arm wave	27	Object move	31	-0.52	0.01	0.04	0.83	0.94	<0.001	0.95	<0.001	0.75	0.03	3.96	0.32
Object move	28	Arm swing	30	-0.41	0.03	0.13	0.50	0.94	<0.001	0.95	<0.001	0.88	0.16	4.12	0.39
Arm swing	29	Tandem walk	29	-0.29	0.13	0.23	0.24	0.95	<0.001	0.95	<0.001	1.02	0.49	4.4	0.51
Tandem walk	30	Bow	28	-0.36	0.05	0.15	0.45	0.95	<0.001	0.95	<0.001	1.02	0.38	4.4	0.46
Bow	31	Stomp 2-feet alternate	27	-0.41	0.02	0.07	0.72	0.94	<0.001	0.94	<0.001	1.02	0.38	4.41	0.41
Stomp 2-feet alternate	32	Push	26	-0.35	0.05	0.07	0.73	0.94	<0.001	0.95	<0.001	1.04	0.28	4.46	0.39
Push	33	Leg swing	25	-0.31	0.08	0.05	0.81	0.95	<0.001	0.95	<0.001	1.05	0.23	4.48	0.35

Order of gesture types				Spearman's correlation test for d				Spearman correlation tests for control analysis for d				L for d			
Gesture type (low to high d)	i (low to high d)	Gesture type (high to low d)	i (high to low d)	r_s (low to high d)	p	r_s high to low d	p	r_s (low to high d)	p	r_s (high to low d)	p	L (low to high d)	p	L (high to low d)	p
Leg swing	34	Feet shake	24	-0.27	0.13	0.02	0.91	0.95	<0.001	0.95	<0.001	1.07	0.21	4.51	0.32
Feet shake	35	Object shake	23	-0.23	0.18	-0.01	0.98	0.95	<0.001	0.95	<0.001	1.09	0.18	4.54	0.29
Object shake	36	Embrace	22	-0.16	0.34	0.10	0.64	0.95	<0.001	0.95	<0.001	1.21	0.34	4.7	0.35
Embrace	37	Head nod	21	-0.18	0.28	0.08	0.74	0.93	<0.001	0.95	<0.001	1.22	0.26	4.7	0.3
Head nod	38	Throw object	20	-0.15	0.36	0.05	0.84	0.93	<0.001	0.95	<0.001	1.24	0.24	4.73	0.28
Throw object	39	Side roulade	19	-0.20	0.21	-0.07	0.77	0.92	<0.001	0.95	<0.001	1.24	0.18	4.74	0.22
Side roulade	40	Reach	18	-0.19	0.25	-0.13	0.60	0.92	<0.001	0.95	<0.001	1.26	0.15	4.75	0.18
Reach	41	Arm shake	17	-0.14	0.38	-0.02	0.94	0.92	<0.001	0.94	<0.001	1.35	0.23	4.88	0.22
Arm shake	42	Stiff walk	16	-0.12	0.46	-0.07	0.79	0.92	<0.001	0.93	<0.001	1.38	0.2	4.92	0.19
Stiff walk	43	Pirouette	15	-0.15	0.33	-0.20	0.49	0.91	<0.001	0.94	<0.001	1.38	0.16	4.92	0.13
Pirouette	44	Hide face	14	-0.19	0.23	-0.35	0.22	0.91	<0.001	0.94	<0.001	1.39	0.13	4.93	0.08
Hide face	45	Bite	13	-0.23	0.14	-0.63	0.02	0.90	<0.001	0.93	<0.001	1.39	0.1	4.93	0.04
Bite	46	Grab	12	-0.18	0.23	-0.58	0.05	0.90	<0.001	0.91	<0.001	1.48	0.15	5.07	0.05
Grab	47	Grab-pull	11	-0.11	0.48	-0.48	0.14	0.90	<0.001	0.89	<0.001	1.77	0.55	5.82	0.15
Grab-pull	48	Gallop	10	-0.74	0.62	-0.45	0.19	0.90	<0.001	0.92	<0.001	1.82	0.57	6.05	0.16
Gallop	49	Somersault	9	-0.49	0.74	-0.60	0.09	0.91	<0.001	0.89	<0.01	1.84	0.54	6.18	0.12
Somersault	50	Roll over	8	-0.02	0.88	-0.69	0.06	0.91	<0.001	0.92	<0.01	1.88	0.53	6.36	0.07
Roll over	51	Head stand	7	0.01	0.98	-0.76	0.05	0.91	<0.001	0.96	<0.001	1.92	0.51	6.52	0.02
Head stand	52	Dangle	6	0.03	0.84	-0.84	0.04	0.90	<0.001	0.99	<0.001	1.98	0.5	6.61	0.01
Dangle	53	Object in mouth	5	0.08	0.56	-0.72	0.17	0.91	<0.001	0.98	0.01	2.44	0.91	7.94	0.07

Order of gesture types				Spearman's correlation test for d				Spearman correlation tests for control analysis for d				L for d			
Gesture type (low to high d)	i (low to high d)	Gesture type (high to low d)	i (high to low d)	r_s (low to high d)	p	r_s high to low d	p	r_s (low to high d)	p	r_s (high to low d)	p	L (low to high d)	p	L (high to low d)	p
Object in mouth	54	Hand on	4	0.10	0.47	na	na	0.91	<0.001	na	na	2.5	0.87	na	na
Hand on	55	Leaf clipping	3	0.12	0.39	na	na	0.90	<0.001	na	na	2.61	0.86	na	na
Leaf clipping	56	Directed push	2	0.08	0.56	na	na	0.89	<0.001	na	na	2.62	0.72	na	na
Directed push	57	Water splash, 1 hand	1	0.03	0.84	na	na	0.88	<0.001	na	na	2.63	0.57	na	na
Water splash, 1 hand	58		0	-0.01	0.97	na	na	0.86	<0.001	na	na	2.65	0.42	na	na

9

10

11

12 **References of the Electronic Supplementary Material**

- 13 1. Hobaiter C, Byrne RW. 2011 The gestural repertoire of the wild chimpanzee. *Anim.*
14 *Cogn.* **14**, 745–767. (doi:10.1007/s10071-011-0409-2)
- 15 2. Conover WJ. 1999 *Practical nonparametric statistics*. New York: Wiley.
- 16 3. Rice JA. 2007 *Mathematical statistics and data analysis*. 3rd edn. Belmont, CA:
17 Duxbury.
- 18 4. DeGroot MH. 1989 *Probability and statistics*. 2nd edn. Reading, MA: Addison-
19 Wesley.

20

21